The Taxonomy of *Haastia*

(Compositae - Asteraceae)

A Thesis submitted in partial fulfilment of the
requirements for the Degree of
Master of Science in Botany
in the
University of Canterbury
by

M. J. Todd

University of Canterbury
1996

Frontispiece: *Haastia pulvinaris* var. *minor*, Mt. St. Patrick, North Canterbury. The St. James Range in the distance.

For My Parents

who taught me to appreciate

the Great Outdoors

Table of Contents

List of Figures and Tables

List of Figures

List of Tables

Abstract

The taxonomy of the genus *Haastia* is investigated in preparation for a formal revision. Morphological and anatomical character states are analysed using numerical phenetic techniques; biochemical, ecological and geographical information is also utilised.

Two new taxa are proposed; one new species and a new variety of *Haastia sinclairii*. It is recommended that *Haastia pulvinaris* var. *minor* be promoted to the rank of species. All other taxa should retain their current status.

Natural hybridisation is discussed. All taxa are keyed and described.

1 Introduction

1.1 Introduction to Taxonomy

Taxonomy is the science of classification, which is the ordering of groups of organisms known as taxa (*sing.* taxon). Although the uses of modern taxonomy are many and varied, all may be summarised in three main aims, according to Davis & Heywood (1963: 2)

1. To provide a convenient method of identification and communication.
2. To provide a classification which as far as possible expresses the natural relationships of organisms.
3. To detect evolution at work, discovering its processes and interpreting its results.

Stuessy (1990: 9) suggests that taxonomy *sensu stricto* deals only with the empirical procedures of classification, and with the theory of identification and nomenclature. Studies of phylogeny and of evolutionary processes, although related to taxonomic matters, are separate. Stuessy goes on to point out that all of these are, however, included in the encompassing field of biosystematics, or 'the study of biological diversity', of which they are complementary aspects.

Regardless of the semantics, the results of taxonomic research are utilised throughout the fields of biology, even if only incidentally. It is therefore the responsibility of the taxonomist to ensure that the contents of these results are as

explicit and as up-to-date as possible. The best method of achieving this is through the presentation of taxonomic monographs and revisions. The primary object of both dissertations 'is to delimit the taxa clearly (particularly species), to group them in a natural manner, and to provide means of identification' (Davis & Heywood, 1963: 293). A monograph should go further than this, in an attempt to synthesise all the available information pertaining to a group, including speculation as to the probable phylogeny, but revisions are more practical in nature, and are usually concerned mainly with the details of classification.

1.2 The Need for Taxonomic Revision

Like all the natural sciences, taxonomy is a dynamic discipline, and classifications are constantly changing and expanding by a variety of processes, at least as far as the biological sciences are concerned. These processes may be of a practical or theoretical nature.

On a practical level, our knowledge of the structure and function of organisms is continually being increased as new discoveries are made. As our pool of knowledge expands and new evidence is made apparent, our perception of the taxa and their relationships to one another also changes (Stuessy 1990: 4). For example, over the last twenty years the fields of molecular genetics and chemotaxonomy have flourished, producing a wealth of data and information (Gardner & Snustad 1984, Harborne & Turner 1984, Stuessy 1990: 313, 329). Using this new information, it has been possible to gain entirely new insights into the relationships between taxa previously classified only by morphology, anatomy, and occasionally cytology. An example of this may be seen in the chemotaxonomic evidence presented by

Markham *et al.* (1985),relating to the revision of the Podocarpaceae by de Laubenfels (1969).

On a more theoretical level, the methods of analysis of data and the basis for classification are often influenced by dominant trends in thinking; and at times one technique may be more fashionable than others. As the basis of a classification changes, the classification may also change as emphasis is moved to new considerations. The best example of this occurs in the contrast between 'phylogenetic' and 'phenetic' classifications (Stuessy 1990). Phylogenetic taxonomists, including the advocates of cladistic techniques, maintain that only by tracing the evolutionary pathways may the relationships between related taxa be known, and that this may be achieved through the polarisation of characters into the categories of 'primitive' and 'derived', and the identification of synapomorphies (derived character states shared between two or more taxa) (Hennig 1965). Pheneticists and numerical taxonomists argue that it is impossible to know with any degree of certainty the phylogeny of a taxon, and that the most suitable means of classification is the analysis of the degree of overall similarity between any two taxa (Davis & Heywood 1963: xviii; Sokal & Sneath 1963: 7; Kavanaugh 1977) (N.B. this is <u>not</u> a view that is universally favoured by phenetic taxonomists (Stuessy 1990: 25)). During the 1960s and '70s, this latter technique was commonly used, particularly with the increasing utilisation of computers to process large amounts of data (Duncan & Baum 1981). However, during the late '70s and 1980s, cladistic analysis began to have a marked impact (Duncan & Stuessy 1985; Stuessy 1990: 130), although the claim that the method heralded a revolution in taxonomy (Funk & Brooks 1981) may be regarded as an exaggeration (Stuessy 1990: 130).

A complicating factor, that has little to do with the methods or theory of analysis, is related to the natural evolution of taxa, particularly through the processes of hybridisation and speciation. Evolutionary processes, while proceeding at a much slower rate than advances in knowledge and changes in thinking, have a profound effect upon the relationships between taxa. For example, catastrophic events may often act as catalysts for rapid speciation and hybridisation through sudden changes in both the form and intensity of selection pressure (Eldredge & Gould 1972). It is suggested that up to 80% of plant species of the world could be of hybrid origin (Grant 1971), mainly by allopolyploidy (Reiseberg & Ellstrand 1993, Arnold 1994). Even if the true number were half Grant's approximation, hybridisation and the accompanying speciation processes potentially play a significant role in the composition of global flora, which may be considerably more dynamic than is readily apparent. Therefore, even if the mechanics of classification should remain static, the subject matter itself may be altered through genetic modification. This is particularly pertinent to infraspecific taxa, such as varieties or sub-species, that are subject to a greater incidence of hybridisation than taxa of higher categories (Stuessy 1990: 192).

With such a potential for change in the arrangement of organisms, it may be seen that taxonomists must constantly keep abreast of new developments and ideas in order to sustain the validity of their work.

Unfortunately, given the vast number of species of plants and animals in the world, it is clearly an impossible task to keep more than a necessary handful totally up-to-

date at all times. Other species must wait to be revised only occasionally, as time and resources allow. Accordingly, the relationships amongst and within many taxa of plants and animals are still obscure and often incomprehensible.

1.3 Definitions and Terms

1.3.1 The Definition of 'Species'

While 'taxon' is a general term that may be applied to any group of organisms, a 'species' is rather more difficult to define. Controversy over exactly what constituted a species led Stebbins (1950) to comment that there were almost as many different definitions of species as there were evolutionary biologists. However, only three definitions are of relevance to this discussion. The first is the morphological species concept (also known as the classical species concept (Burger 1975)), which is that most easily applied for taxonomic purposes (Stuessy 1990: 171). According to this definition, species are

> "the smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotypes." (Du Rietz 1930, cited in Davis & Heywood 1963: 92 and Stuessy 1990: 172)

Using this definition, a taxon is only required to be phenetically distinct, and recognised as such, to be called a species. The character, or even the existence, of the evolutionary forces that may (or may not) have caused such discontinuity is irrelevant (Heywood 1967, cited in Stuessy 1990: 172). This definition is particularly useful when little is known of either the reproductive biology of the

organism, or of its interactions with other organisms, dissimilar to itself. However, the morphological species concept has even proved its worth in cases where distinction of taxa has been complicated by a high incidence of hybridisation, (e.g. *Quercus* (Burger 1975)).

Despite the practicality and applicability of the morphological species concept, few taxonomists deny the importance of reproductive biology in the delimitation of a species (Littlejohn 1981). Even if such information is not accessible, it is often taken for granted that phenetic distinction is reflected to a similar degree by the effects of interbreeding and reproductive isolation (Runemark 1961, cited in Stuessy 1990; 172) Where such information is available, the biological species concept, as expounded by Mayr (1942 and 1963), is often emphasised. Mayr's definition follows:

> "a group of actually or potentially interbreeding populations, which are reproductively isolated from other such groups." (Mayr 1940, cited in Mayr 1963: 19).

A difficulty is encountered in the precise meaning of the term 'reproductive isolation'. There are a number of forms of reproductive barriers, both pre- and post-fertilisation, and the effectiveness of isolation varies not only between these forms, but also between the systems that they are applied to (Ehrlich 1961). For example, inter-specific hybridisation is more common in the plant kingdom than in the animal kingdom (Heiser 1973, Stuessy 1990: 173) to which Mayr's concept was originally applied. Under the biological concept, species that commonly give rise to hybrids

should technically be denied that status, despite being recognised as morphologically distinct. "To deny many of these forms specific rank just because they can interbreed is to force nature into a human definition, instead of adjusting [the] definition to the facts of nature." (Huxley 1942, cited in Davis & Heywood 1963: 96).

Perhaps a more suitable concept to adopt is the 'species-standard' concept, as proposed by Rollins (1952). This advocates the determination of a morphological species as a 'standard', or reference point, the integrity of which is then rigorously tested by a variety of techniques, ranging from comparisons of phenetic character states between standards, to experimental outcrossing and transplanting. Futuyma & Mayer (1980) present a similar idea, although somewhat modified. Under their proposal, a species may be defined as:

> "a group of populations whose evolutionary pathway is distinct and independent of that of other groups. Such groups reach species status when shown to be reproductively isolated under sympatric conditions, i.e. given the chance to interbreed, or otherwise retain their separate identity".

This last definition retains the practicality of the morphological concept while recognising the importance of the biological concept and reproductive isolation, and also allows for such complications as hybridisation and geographical variation. Therefore, this is the species concept that shall be used for the purposes of this thesis.

1.3.2 'Variety' and 'Subspecies'

There is a large degree of confusion amongst taxonomists as to the delimitation and application of the terms 'variety' and 'subspecies' (Stuessy 1990: 182). Usage of the terms fluctuates widely; sometimes only one or the other is used to classify infraspecific variation, sometimes both are used concurrently. Stuessy (1990) attempts to clarify the situation by suggesting the following criteria of distinction for the utilisation of each rank (p. 189). Comparisons are made in reference to the type of the species.

> *Subspecies:* several conspicuous morphological differences; largely allopatric or peripatric; hybridisation possible in contact zones.

> *Variety:* few conspicuous morphological differences; largely allopatric with overlap; hybridisation probable in overlap zones.

The first two criteria, those concerning morphological divergence and geographical distribution, are the most easily applied, as Stuessy freely admits (1990: 190), and therefore should be utilised as the primary indicators of rank. The last criterion, that concerning the likelihood of hybridisation, is also difficult to measure accurately, and should only be regarded as a secondary indicator for this reason.

For this thesis, the ranks of subspecies and variety will be utilised with these criteria in mind. The term 'form' will also be used, but only informally, or when referring to a taxon, or taxa, of uncertain status.

1.4 Composite Taxonomy in New Zealand

The Compositae are well represented in New Zealand, with genera and species of six of the ten tribes (*sensu* Bentham 1873) native, many of them endemic (Allan 1961). However, due to the relatively short history of biological research in New Zealand, the relationship of many of the native species to one another and to other members of their tribes elsewhere in the world is not fully understood. This applies particularly to the status of the New Zealand members of the tribe Inuleae, most of which belong to the subtribe Gnaphaliinae (*sensu* Bentham 1873). Since Bentham's (1873) treatment of the Compositae, a number of revisions relating to the Inuleae have been published. One of the most comprehensive of these, by Merxmüller *et al.* (1977) compresses Bentham's nine sub-tribes into three, using floral and pollen morphology, and chromosome counts, as particular diagnostic characters. Anderberg (1989) approaches the task from a different perspective. Deeming the Inuleae paraphyletic, his revision splits Bentham's tribe into three new tribes. Although the number of resultant groupings are the same, an entire rank separates these two revisions at this level..

All of the indigenous gnaphalioid genera of New Zealand fall into the largest of the three new tribes resulting from Anderberg's treatment, the Gnaphalieae, but further divisions at the sub-tribal level separate taxa previously believed to be closely related (Anderberg 1991). Until such a time as these anomalies have been satisfactorily explained, it may be prudent to approach this revision with caution.

As far as the majority of the New Zealand native genera of the Inuleae are concerned, there is little fracturing of the inter-generic and inter-specific

relationships elucidated by Bentham's treatment (1873) under the revision of Merxmüller *et al.* (1977), despite the shuffling of the taxa of greater rank in the hierarchy. *Craspedia*, a genus that was regarded by Bentham as a member of the Australian based sub-tribe Angianthinae, is now included in the Gnaphaliinae (*sensu* Merxmüller *et al.* 1977) as part of the less formal *Angianthus* complex. The composition of the two large, widespread genera, *Gnaphalium* and *Helichrysum*, has also undergone a series of changes as various species have been transferred into, out of, and between the two genera (e.g. Drury 1970, Hilliard & Burtt 1981).

A feature of the revision of Merxmüller *et al.* that is of more immediate interest is the treatment of the genus *Haastia*. It is suggested that the genus be split in two, with a single species, *Haastia pulvinaris*, being referred to the Inuleae (Merxmüller *et al.* 1977), although no particular reason is given for this. No suggestion is made of the fate of the other two species, *Haastia recurva* and *Haastia sinclairii*, other than the implication that they be placed in another, possibly new, genus. Merxmüller's suggestion was followed in part by Webb *et al.* in volume IV of the *Flora of New Zealand* (1988), transferring the entire genus to the Inuleae. This treatment was questioned by Breitwieser (1993) on the basis of leaf anatomy, but no alternative was offered.

A recent publication by Bremer (1994: 272) places *Haastia* in the Asteroideae, a group of eight genera as yet unassigned to a tribe. A major feature of this group is the presence of two style types:

(a) robust, with separate stigmatic lines, and obtuse hairs confined to a short conical appendage.

(b) style branches very slender, with entire stigmatic areas and dorsally scattered obtuse hairs.

Clearly, the situation requires clarification. The genus is currently referred to the Inuleae, but may not belong there. It is not even certain that the genus is monophyletic. One aim of this thesis is to address the second of these issues. This will be achieved through a detailed investigation of the species of *Haastia*, gauging and elucidating their similarities and differences, and their relationships to one another.

1.5 Haastia *Hook. f. 1864*

The genus *Haastia* was first published in Sir Joseph Hooker's '*Handbook of the New Zealand Flora*' (1864), and named by Hooker for the noted botanist and geologist Julius von Haast. Hooker described the genus as one of alpine herbs, restricted to the scree slopes and rocky outcrops of the dry eastern ranges of the Southern Alps. The distinguishing features of the genus included solitary, terminal, sessile capitula, the thick fulvous layer of woolly hairs on the upper surface of the leaf as well as the lower, and the club-like structure of the pappus hairs (Hooker 1864).

Both the female and hermaphrodite florets are numerous (Hooker 1864), and numbers may vary according to the size of the capitulum, although the female florets seldom outnumber their hermaphrodite counterparts. The anthers are sagittate, with rudimentary tails, a feature common in the Astereae, but not known elsewhere in the Inuleae (Bentham 1873). The bracts of the capitulum are sepaloid, and form two imbricate series (Hooker 1864).

While a number of secondary metabolites are shared with many members of the Inuleae, and also with taxa belonging to other tribes, all the species of *Haastia* share a small group of flavonoid compounds that are unknown amongst the gnaphalioid genera of New Zealand (Breitwieser & Ward 1993).

Following Hooker, the genus has traditionally contained three species: *Haastia pulvinaris*, *H. sinclairii*, and *H. recurva*.

1.5.1 Haastia pulvinaris *Hook. f. 1864*

This species is the type for the genus, and was first collected by Andrew Sinclair from 'Mowatts Mountain' and the Kaikoura Mountains (Hooker 1864). 'Mowatts Mountain' has been tentatively identified as Altimarloch, a peak on the station of the same name, owned by the Mowat family for much of the latter half of the 19th century (Kennington 1978). The species is found east of the main divide from lat. 41° to 42° 30' S (Allan 1961). The species is restricted to the alpine zones (*sensu* Burrows 1967) where it may be found most commonly on the more stable screes and rock fields. Populations seldom extend below 1300m (4300') above sea level (Mark & Adams 1973).

As the name suggests, the plant is pulvinate in habit, forming large cushions (Hooker 1864) (Fig 1.1), often up to 2m in diameter (Allan 1961). When this is coupled with its woolly appearance, the reasons for the common name of 'giant vegetable sheep' become apparent. The leaves are densely imbricate, spiralling tightly around the branch to form a cylindrical structure *c* 2cm in diameter (Allan 1961). The branches are themselves closely packed and of a more or less even length, such that a solid

Figure 1.1: Habit of *Haastia pulvinaris*, Tapu-ea-nuku.

Figure 1.2: Staircase Stream, site of the Tapu-ea-nuku populations of *Haastia pulvinaris* var. *pulvinaris* and *Haastia pulvinaris* var. *minor*.

surface, practically impervious to the elements, is presented (Hooker 1864). All the viable foliage is found on the exterior only of the plant; so that no light penetrates within, and the older leaves lower down the branch quickly senesce (Low 1899).

Only a narrow lamina is exposed (Low 1899), seldom more then 5mm in length but often over 15mm in width, and "concealed by a dense brush of ... fulvous hairs" (Allan 1961). In order to maximise the photosynthetic area available, the upper surface of the lamina is convoluted into a number of papilla-like projections (Low 1899). The leaf is served by three major veins, or nerves, that rapidly divide to form a reticulate network covering the lamina. In section, it may be seen that each of the nerves is associated with a large, abaxial resin canal (Low 1899; Breitwieser 1993) that extends the length of the leaf to the stem.

The capitulum is usually approximately 5mm in diameter (Allan 1961). Invariably, they are submerged amongst the foliage such that only the upper portion is exposed. The corolla of the hermaphrodite floret is perfect, while the corolla of the female florets is reduced, and the "style-arms far-exserted" (Allan 1961). The pappus hairs, somewhat thickened at the top (Hooker 1864; Allan 1961), are free at the base on both floret types (Hooker 1864).

Haastia pulvinaris *var.* minor *Laing 1912*

The first description of this variety (Fig 1.3) was made by Laing (1912), from specimens collected on the peak of Mt. Princess (Allan 1961). The branchlets are slimmer then those of the parent species, seldom exceeding 15mm in diameter (Laing 1912; Allan 1961). The tomentum is paler (Laing 1912) and less dense. The

pappus hairs are slender and more or less uniform for their entire length (Laing 1912).

The range of the variety is similar to that of the type variety, being found throughout Marlborough and south-east Nelson (Mark & Adams 1973).

Figure 1.3: *Haastia pulvinaris* var. *minor*, Mt. St. Patrick.

1.5.2 **Haastia recurva** *Hook. f. 1864*

This species is also restricted in its range, being found only in the mountains of Marlborough, Nelson and Canterbury, where it is known to grow as far south as Mt. Hutt. The type location is Tarndale (Allan 1961), in southern Nelson where it was

collected by Sinclair. *H. recurva* may commonly be found growing on scree or shingle, where it forms dense mats (Hooker 1864) (Fig 1.4).

The leaves of *H. recurva* are larger then those of *H. pulvinaris*, with the lamina often reaching 4/5" (20mm) in length (Hooker 1864; Allan 1961). However they are not so closely packed (Hooker 1864), and older leaves viable for a greater length of time. The lamina, obovate in shape, is strongly recurved (Hooker 1864; Allan 1961). The leaf is served by at least three major nerves that divide to form a network of reticulate venation similar to that of *H. pulvinaris*.

The capitula are of similar dimensions to those of *H. pulvinaris*, although tending to a narrower receptacle(Allan 1961). The corolla of the female florets is also reduced, but not to such a marked degree. The pappus hairs are connate at the base (Hooker 1864).

Haastia recurva *var.* wallii *Ckn. 1918*

The type specimen for this variety was collected by Professor Wall from the peak of Mt. Fyffe, in the Seaward Kaikoura range. However, Cockayne (1918), in his description of the variety, noted that Wall's find was an isolated plant and not collected from elsewhere in the vicinity. The main range of the plant is further west, around the heads of the Awatere and Acheron rivers, in south western Marlborough (Cockayne 1918). The variety is distinguished from the type form by the smaller size(Allan 1961) and darker green colour of the leaves (Fig 1.5). The capitula are also of a lesser diameter. The involucral bracts are apiculate (Allan 1961).

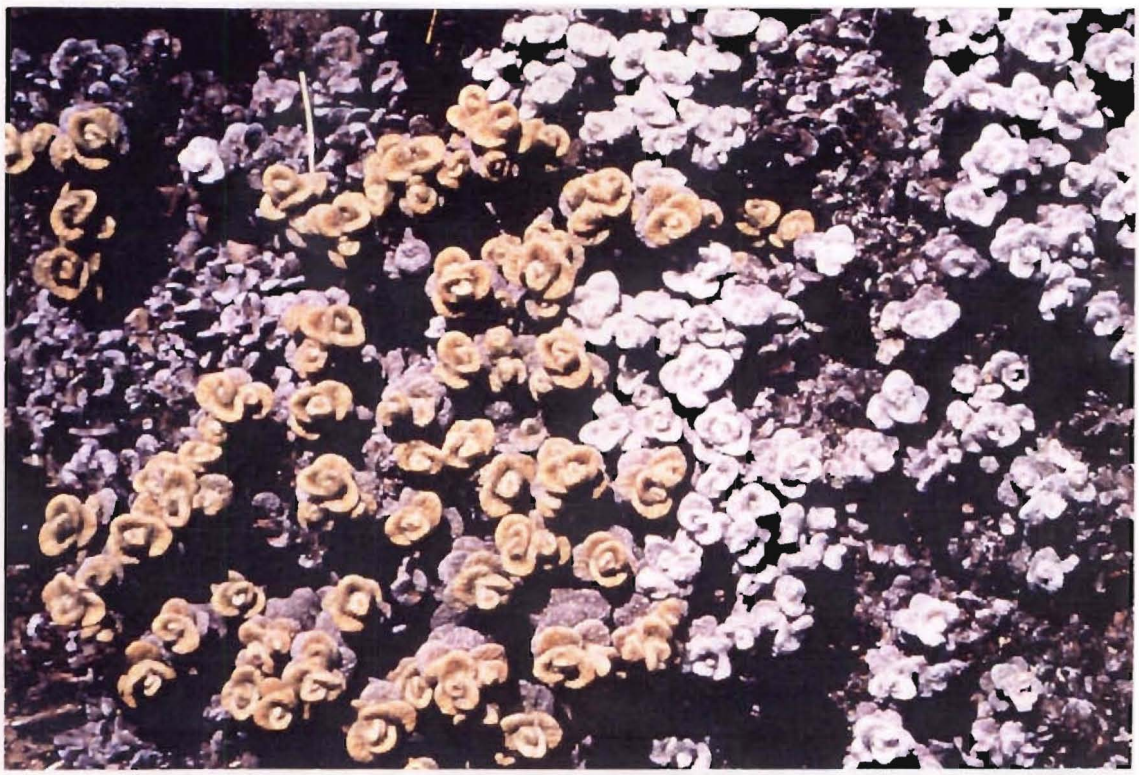


Figure 1.4: Habit of *Haastia recurva*, Poulter Hill. Both forms of the colour polymorphism are present.

Figure 1.5: Habit of *Haastia recurva* var. *wallii*, Mt. Schiza.

1.5.3 Haastia sinclairii *Hook. f. 1864*

The type specimen for this species was collected from the Wairau Pass (Allan 1961), again by Sinclair. The range is far larger then that of either *H. pulvinaris* or *H. recurva*. *Haastia sinclairii* shows tolerance for a variety of habitats and climates, and may be found wherever there is broken or rocky ground at suitable altitude throughout the South Island, "from lat. 41° to 45°" (Allan 1961), including high rainfall areas such as NW Nelson and Fiordland.

H. sinclairii is also the most variable of the three species in habit. Specimens may be "sparingly to much branched, decumbent to sub-erect" (Allan 1961), with stems reaching lengths of 30 cm (Allan 1961). The leaves are the largest of the three species, up to 15mm in width and reaching lengths of 35mm (Allan 1961). Although imbricate and semi-erect, the leaf arrangement is the most lax of the three species (Hooker 1864), and there is little leaf senesence away from the branch ends. Possibly reflecting this, the upper surface of the leaf is only slightly rugose (Allan 1961). The obovate lamina is the largest part of the leaf. Five to ten nerves form the base of the reticulate network of veins throughout the lamina (Hooker 1864; Allan 1961).

The capitula are variable in size (Hooker 1864), up to *c.* 30 cm long (Allan 1961). The receptacle is usually of a narrower diameter, around 3-5 mm in diameter (Allan 1961). The pappus hairs are not fused to one another at the base (Hooker 1864).

Figure 1.6: Habit of *Haastia sinclairii*, Broken River skifield

Figure 1.7: Habit of *Haastia sinclairii* 'Potts', Mt. Potts.

Figure 1.8: Habit of *Haastia sinclairii* var. *fulvida*, Mt. Bonpland

Haastia sinclairii *var.* fulvida *Allan 1961*

The type locality of this variety is Gertrude Saddle, in Fiordland, whence the type specimen was collected in 1939 by Lucy Moore. The range is restricted to Fiordland and western Otago, occurring no further north then Lake Wanaka (Allan 1961).

The leaves are narrow, only 5-10 mm wide, although still reaching lengths of *c.* 30mm (Allan 1961) (Fig 1.8). There is only a sparse covering of short hairs on the upper surface of the leaf, resulting in a yellow-green colour for the plant. The

capitula are smaller then those of the type variety, seldom exceeding 20mm in diameter (Allan 1961). The involucral bracts are *c.* 10mm long, with broad margins (Allan 1961).

1.5.4 Other taxa

Three species are described in the literature that are, for a variety of reasons, no longer considered as members of *Haastia* and have been excluded from this investigation.

Haastia loganii (Buchanan 1882) was initially collected from Mt. Holdsworth in the Tararua range, and was described as a small patch plant with reddish florets. In revision, the taxon was referred firstly to *Helichrysum* by Kirk (1899), and then later to *Raoulia* by Cheeseman (1925). Finally, it was recognised as a hybrid of *Raoulia rubra* and *Leucogenes leontopodium* by Cockayne & Allan (1934, cited in Allan 1961).

Haastia montana (Buchanan 1887) was described from material collected on Mt. Alta as having large upright leaves, small capitula, and greatly reduced involucral bracts. The status of this taxon remains uncertain, as the plant appears to have never been relocated in the field since Buchanan's original collection and description (Cheeseman 1925).

Haastia greenii Hook .f. 1899, collected by the Rev. Green from the slopes of Mt. Cook, was described as being a small, densely tufted cushion plant (Kirk 1899). The

flowers were unknown at the time of description. The species was deemed synonymous with *Raoulia eximia* by Allan (1961).

In addition, an unknown taxon was recently noted and photographed by Ann Cartman, of the Canterbury Alpine Garden Society, from snow hollows at the top of the Erewhon Park ski-field, in the Potts Range (Fig 1.7). The plant is similar in form to *H. sinclairii*, but is much green in colour, and the capitula are not sessile, but held a few centimetres above the surface of the plant by floral branchlets extended through the elongation of the leaf internodes (pers. comm. Dr. J. Ward).

1.5 Summary of Issues

In summary, there are three issues that require particular attention. The first of these is the relationship between the two taxa of *Haastia pulvinaris*. The two are commonly found growing close to one another, if not directly interacting, yet have remained morphologically distinct. According to the criteria outlined by Stuessy (1991), not only should varieties be largely geographically separate, but they should differ in only one or two structural details. The status and relationship of these two taxa needs investigation.

Secondly, the taxonomy of *Haastia sinclairii* is complex. There is a large degree of morphological variation within the species that may well mask distinct taxa. This variation requires evaluation in relation to geographical and ecological occurrence.

The previously unknown taxon from Mt. Potts requires assessment and description. The elevated capitulum is unknown elsewhere in the genus, and there are a number

of morphological differences between it and *H. sinclairii,* to where the plant has temporarily been referred. It's status in the genus will be closely scrutinised.

In addition, all other taxa, including *H. recurva* and its single published variety, will be routinely investigated so that as complete a comparison as possible may be drawn between the taxa.

Finally, at the end of the investigation, a key to all species and varieties of the genus will be prepared, and descriptions made of any new taxa.

2 Methods and Techniques

2.1 Field Techniques

2.1.1 Collection of Specimens

Specimens were collected from a broad selection of sites (Fig. 2.1) from the entire range of the genus in order to sample as much of the diversity both between and within the species as possible. All three of the known species were extensively sampled, along with any unusual or previously unseen (or at least, unpublished) variations. The only described taxon unsampled was *Haastia. montana* (published from a single specimen (Kirk 1899) and never relocated (Cheeseman 1925)).

Sites were chosen subjectively; the two main criteria being previous knowledge of the flora, and accessibility. For this reason, many of the chosen sites were found on ski-fields, or close to tramping routes.

The majority of the specimens were collected during the summer of 1994/95, between late November and early April, by Aaron Wilton and myself. Supplemental material was collected during the summer of 1995/96. Other specimens were collected by Aaron Wilton over a similar period during previous years, and by Dr. Ward, Dr. David Norton, and Hamish Cochrane . Such a defined collecting period was made necessary by the relatively short time between the spring thaw and the first snow of autumn, during which the flowering and growing seasons of *Haastia*, along with many other alpine plants, are completed. The plants are buried by snow at all other times of the year.

1. Kakapo Peak
2. Tapu-ea-nuku
3. Mt. Schiza
4. Mt. Barefell
5. Mt. Fyffe
6. Balaklava Ridge
7. Mt. Southey
8. Mt. Princess
9. Mt. McCabe
10. Mt. Terako
11. Mt. St. Patrick
12. Mt. Edison
13. Poulter Range
14. Poulter Hill
15. Craigieburn skifield
16. Broken River skifield
17. Mt. Hutt
18. Mt. Potts
19. Ohau skifield
20. Mt. Bonpland

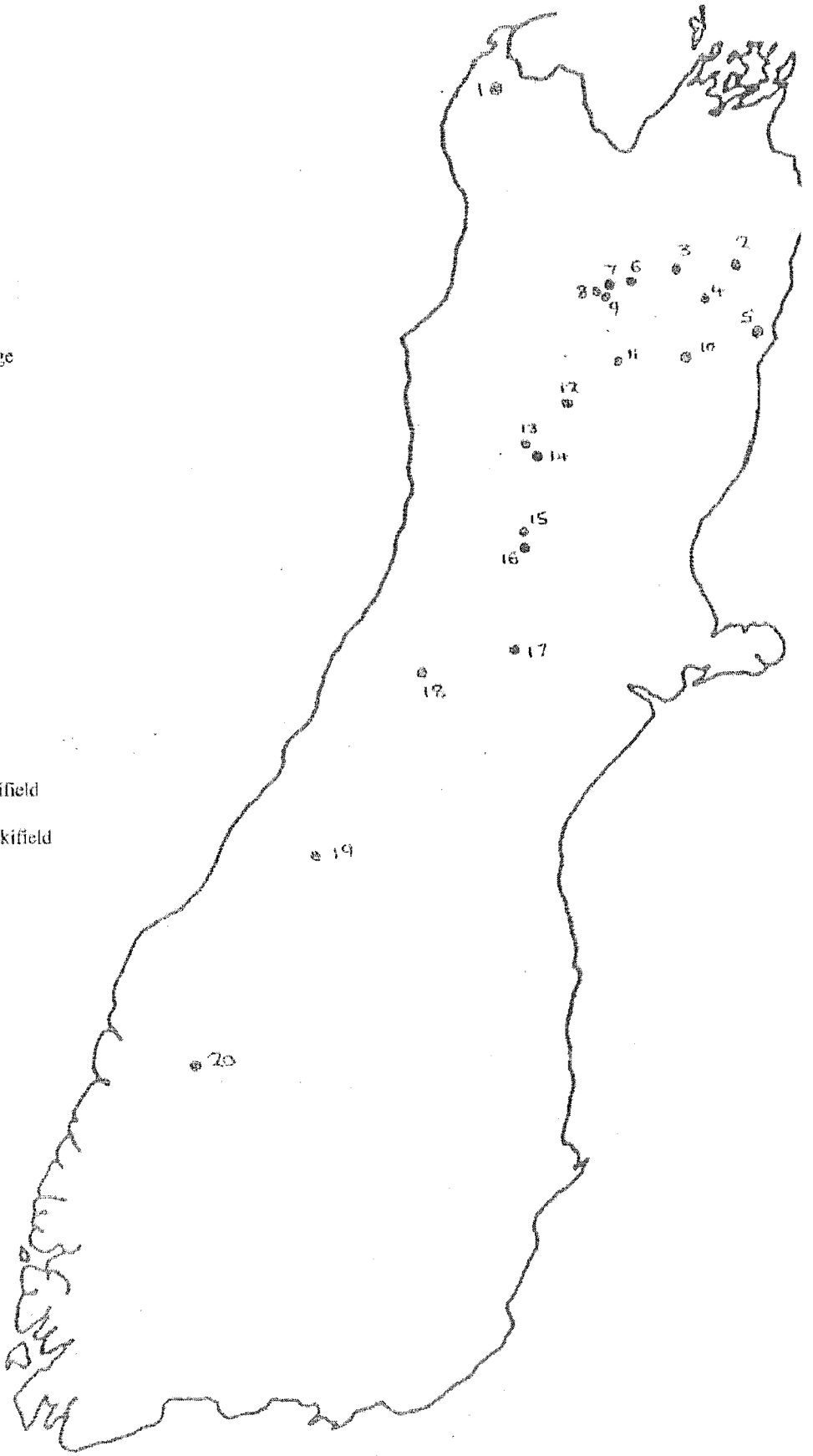


Figure 2.1: Map of the South Island showing the locations of all collecting sites.

Collecting trips were deliberately short, generally only one or two days, so that specimens collected could be kept in good condition until preserving. The two longest trips were to the Douglas Range in Northwest Nelson (five days) and to Mt. Bonpland in Fiordland (six days), and specimens were only collected during the latter half of these trips respectively. Where possible, specimens were wrapped in damp sphagnum moss immediately upon collection, in order to further reduce damage through desiccation.

For each specimen collected, notes were taken at the time on the location and altitude of the site, the important features of the habitat, both biotic and abiotic, and on the general growth form of the plant itself. Samples of the leaves and stems were collected from each plant, and, where possible, the roots, rhizomes and floral parts were included. Each specimen was numbered according to the order in which they were collected. A number of plants were sampled from each site in order to fully account for variation, but no more then five from any one population. Damage to the plants was kept to a minimum as much as possible, although the sampling was destructive by its very nature.

At some sites, extra samples of healthy leaves were collected in order to provide enough material for flavonoid analysis. Such samples were taken for each of the species, and also for *H. pulvinaris* var. *minor* and the new taxon found on Mt. Potts.

In the laboratory, a suitably representative part of each specimen was dried for use as a herbarium voucher, while the rest was preserved in formalin acetic alcohol (FAA).

Some specimens were also used for propagation in the university glasshouses. Samples gathered for flavonoid analysis were freeze-dried using an Edwards 30P2 centrifugal freeze-drier, and then stored in sealed heavy paper bags.

2.1.2 Phenology

Thirty plants from each of the two *Haastia pulvinaris* populations at the summit of Mt. St. Patrick were marked using aluminium pegs. The pegs were colour-coded: yellow for the plants of the var. *pulvinaris* population, red for var. *minor*. All thirty of the plants of var. *pulvinaris* were located on the north-west face of the peak, as this population is apparently restricted to this habitat. Five of the marked var. *minor* plants were also found on this face, with the remainder on the south-east side.

The site was visited once every two weeks from the start of flowering, in late December, 1994, until snow coverage made further observations impractical, in mid-April, 1995. On each visit the approximate percentage of open flowers and ripe seed, relative to the total potential production, was recorded for each plant. This was measured by estimating the surface area of the plant, the area covered by open capitula, and the number of flowers producing ripe seed. Each plant was given a score between 0 and 3 for both flowers and seed. A zero rating was given for no production, a one for less then five percent (few), a two for less then twenty-five percent (some), and a three given for twenty-five percent or greater (many). For example, a large plant, over a metre in diameter, scored only a one, for few flowers, if it had twenty capitula scattered over its surface. A smaller plant, a bare thirty centimetres across, scored a two, or even a three, for the same number of flowers.

On a later visit, if two or three capitula on each plant were producing viable seed, then each plant received a two for the seed rating.

2.2 Laboratory Techniques

2.2.1 Dissection of Vegetative and Floral Material

All vegetative and floral material examined came from specimens earlier preserved in FAA., and was dissected and studied in small baths of either this medium, or its base of 70% alcohol, in order to avoid desiccation due to extended exposure to air. Dissections were carried out under a Wild stereoscopic light microscope.

In a number of instances, leaf material could not be closely examined until the dense covering of hairs on the adaxial surface of the lamina was removed. This was achieved by carefully shaving the leaf surface with a sharp scalpel blade. Shaving strokes were made with the lie of the hairs, from the lamina base to the apex, in order to minimise damage to the epithelium.

2.2.2 Scanning Electron Microscope Techniques

In a number of instances, the degree of magnification available on the light microscope was insufficient for studying micro-morphological features, such as are found in the structures of the florets. Therefore, these specimens were examined under the Scanning Electron Microscope (SEM).

Critical point drying was chosen as the most suitable method of preparation, as it minimised the risk of cell deformation during the drying process (Turner & Green

1972). The technique used followed that prescribed by Turner & Green (1972), with the exception that CO_2 was used rather then freon, for its greater degree of solubility with water based preservatives (Boyde & Wood 1969).

The specimens were first dehydrated, by immersion in an ascending alcohol series of 30%, 50%, 70%, 85%, 95% and 100% ethanol, and then flushed of the alcohol in a similar ascending amyl acetate series.

The specimens were dried in a CPD750 critical point drier (Emscape Laboratories), and all safety and operating procedures were carried out as per the manufacturers instructions and the standards of the SEM laboratory in the Plant and Microbial Sciences Department. A fume cupboard was used at all stages of the process.

While still well coated in amyl acetate, the specimens were transferred to small glass capsules, open at either end, and secured with fine mesh. These were placed inside the chamber of the vessel, and the vessel lid was sealed. The chamber was then filled with CO_2, and air purged via the outlet valve. The chamber was then pressurised to 750 p.s.i.

After four minutes (rather then the seven specified by Turner & Green (1972), due to the delicate nature of the specimens), the outlet valve was opened for three minutes to allow the chamber to be flushed of the CO_2 and dissolved amyl acetate. The chamber was re-flooded with fresh CO_2 and pressurised once more. During this time, care was taken to remove excess moisture from the outlet valve in order to minimise blockage due to freezing during the flushing of the CO_2.

The cycle of filling the chamber with fresh CO_2, followed by the flushing of the CO_2/amyl acetate mixture was repeated several times, until no more amyl acetate could be detected in the flush. Ten such cycles were required.

When no more amyl acetate could be detected, the chamber was sealed and heated with hot water (60°C). The resulting increase in pressure inside the chamber was unchecked until 1600 p.s.i. was reached. The pressure was maintained at this level through judicious use of the outlet valve, until the entire vessel reached a temperature greater then 32°C. The pressure was then slowly released over ten minutes, and the dried specimens removed.

The specimens were mounted on standard SEM stubs and given a 50nm coating of gold in a Polaron 5000 splutter coater, set at 50 milliamps and 1.2kV for five minutes. The finished stubs were labelled by taxon, and viewed under the SEM.

2.2.3 Preparation and Mounting of Tissue Sections.

In order to measure anatomical characters, several typical specimens of each taxon were selected from a number of populations and tissue samples taken. Only a limited number of specimens could be examined due to time and resource limitations.

Sections were taken from samples mounted in blocks of Technovit resin. The procedures involved in the preparation of the resin blocks were followed as per the manufacturers instructions. The staining of the tissue sections was accomplished

following routine procedure in the histology laboratory of the Plant and Microbial Sciences Department. A fume cupboard and gloves were used at all times during the preparation and handling of the resin and of the stain.

From each plant studied, five specimens of tissue were prepared; one each from the root, stem and leaf sheath, and two from the lamina, at the base and apex.

Tissue samples were prepared for embedding by the processes of dehydration, in order to remove any water residue, and infiltration of the cells with liquid resin. Dehydration was achieved simply by the immersion of samples in an ascending alcohol series of 50%, 80%, 95%, and 100% ethanol, for between twenty minutes and an hour at each stage, depending upon the tissue type. Samples were then transferred to an infiltration solution consisting of the resin, Technovit 7100, and type I of the accompanying hardeners, mixed at a ratio of 100ml.: 1g., and refrigerated overnight.

The next stage of the process involved the mounting of the prepared specimens in the resin blocks. Stem and root blocks were cast in polythene capsules; approximately one centimetre long and four millimetres in diameter, cylindrical, and tapering to a thick point at the cutting end. Leaf samples, being too large for these, were mounted in blocks cast in wider, dish like moulds, and the backing block cast separately in protein capsules.

The embedding solution was prepared by adding type II hardener to the infiltration solution at a ratio of 1:15 parts. Once the embedding solution was prepared, there

was a period of approximately 5-7 minutes to pour it into the moulds and position the samples before the setting process began. Only enough solution was poured into each mould to cover the respective samples, and samples were positioned so that as much of the section of interest was flush with the cutting face as possible. When the samples were positioned, and the embedding solution beginning to set, the moulds were left at room temperature for between one and three days in order to harden.

At the end of this period, the backing resin, Technovit 3040, was mixed at a ratio of two parts powder (by volume) to one part liquid (by volume), and the resulting mixture poured into the top of the mould. As with the embedding resin, the time period between the preparation of the mixture and the first signs of hardening was very short, no longer then two minutes. As noted above, the backing resin for any particular leaf sample was cast separately, and attached to the resin block as it began to harden. Again, a twenty-four hour period was required for setting. Once this had occurred, the moulds were cut away, and the block trimmed to present the optimal cutting face.

Sections were cut from the finished blocks using a glass knife on a microtome set at 5μm, and mounted on sterilised glass slides. This was achieved by the expedient means of floating the section on the surface of a water droplet, and then evaporating the droplet on a hot-plate. In this manner, five leaf sections or twenty stem or root sections, all cut from the same sample, could be mounted on a slide. Two slides were made for each tissue sample.

All tissue sections were stained with Azur II. Slides with mounted sections were immersed in the stain for 12-15 seconds and then rinsed several times in a series of fresh water baths, until all the surplus stain washed out.

Stained sections were protected by cover slips fixed with DePex mounting solution. This also required a twenty four hour period for setting, before the completed slides could be labelled with the name of the taxon, the tissue type, and the specimen number.

2.2.4 Preparation of Chromatograms

The flavonoid compounds of the major taxa were extracted and analysed by two-dimensional paper chromotography (2D-PC) using the techniques of Mabry *et al.* (1970) and Markham (1982).

0.5g of the freeze-dried leaf sample was measured for each of the taxa for which such samples were gathered. This was powdered using a pestle and mortar. When necessary, liquid nitrogen was added to crystallise the cell structure, facilitating the powdering process. This extra nitrogen soon evaporated at room temperature.

The powdered sample was then homogenised for one minute in 20ml MeOH (9:1) using an Ultra-Turrax homogeniser. The mixture was then left for at least six hours to settle and the resultant extract drained off, before the solid was homogenised for another minute in 20ml MeOH (1:1), and the process repeated. The two extracts were filtered through Whatman 54 filter paper, combined, and reduced, at 30°C, to 20% of the original volume in a rotary vacuum evaporator.

At this stage, the volume of the extract was exactly measured, and an equal volume of KCl in solution was added, in order to react with any chloroform and effectively remove it from the mixture. The extract was left on ice for 10-15 minutes to allow this reaction to occur, before being transferred once more to the rotary vacuum evaporator, and totally evaporated.

The resultant solid was redissolved in 2 ml of 80% aqueous methanol, and 200µl aliquots applied to one corner of a sheet of Whatman 3MM chromotography paper. A chromatogram was made of this, firstly by TBA (*t*-BuOH/HoAc/H_2O 3:1:1) over a period of six hours, and then in the second dimension by 15% aqueous acetic acid, left for a similar length of time.

The sheets were air dried, and examined under UV light (366nm) both before and after fuming with ammonia.

2.3 Character Selection

Characters were selected subjectively, according to their ease of measurement and to their taxonomic value. In order to offset as much inherent bias as possible in this selection method, a relatively large number of characters were selected for measurement from a range of data sources. These consisted of both vegetative and floral morphology, and anatomy, along with some geographical, ecological, phenological and biochemical data. In order to further offset sampling bias, characters measurements from any particular population were replicated several times, as far as was possible.

A total of eighteen vegetative characters were scored for each of the sixty five preserved samples, as far as was possible. Sixteen floral characters were measured and scored for those samples with floral material available. From the organ samples prepared, a total of eleven anatomical characters were scored. Characters that were either not applicable or not available for any specimen were scored as "N\A".

The characters selected for analysis are detailed fully in Chap. 3.

2.4 Discussion of Techniques

2.4.1 Collection of Specimens

Field samples were preferred over herbarium specimens, as it was felt by the author that the ease of investigation of fresh material, rather than material distorted by the processes of pressing and drying, more than made up for the effort expended collecting from alpine sites. Herbarium material, while providing vital information on morphology, and also on previous collections, was found to be difficult to interpret fully without prior knowledge of the fresh specimen.

Sites throughout the known range of the genus were carefully selected for sampling following examination of the available literature and herbarium specimens, with particular attention being paid to the most recent material. Older references and herbarium sheets were found to be less precise in their site locations, while material presented during the last twenty years was often accompanied by four or six figure grid references, allowing utilisation of the Survey and Land Information N.Z.M.S. 1

and 260 map series to pinpoint sites. Attention was also paid to accessibility. As noted above, priority was given to sites on or close to ski-fields and tramping routes, at least in the initial stages of collection, as it was considered of greater practicality to collect specimens of the three described species from these sites rather than more remote locations. Sites that were not easily accessible were only considered if they were known to be of special significance, such as type localities or the presence of unusual or uncommon plants, or if no more accessible sites were in the vicinity.

Despite best efforts, on several occasions factors such inclement weather, site remoteness, or simple scarcity of the plant in question (due to a small population size) made collection of more than a handful of specimens from the populations in question unfeasible. Consequently, much of the data pertaining to some populations was measured from only one or two plants, and it had to be assumed that these specimens were typical. Fortunately, this restriction does not happen to apply to the more uncommon taxa, sampled from single sites only. All taxa that were only collected from one site, for one reason or another, were well sampled so that the full range of variation within that population could be evaluated.

Preservation of specimens in the field proved to be of some difficulty. The two greatest problems prior to delivery to the laboratory were damage to the specimen through desiccation and through crushing while being carried out in packs. Packing specimens in bags of damp sphagnum moss provided an efficient solution to these problems, acting as both a water reservoir and as padding against crushing.

2.4.2 Collection of Phenological Data

This investigation was only made at a site where the two forms of *H. pulvinaris* were growing in adjacent populations. A similar investigation was considered for Mt. Potts, where both *H. sinclairii* and the 'Potts' form occur, but access to this site was restricted during the months of January and February by the land-owner, making the necessary fort-nightly visits not possible.

The aim of the investigation was to chart any time lapse between the respective flowering periods of the two populations. Unfortunately, this was made somewhat difficult by the marked disparity in climatic conditions on either side of the peak of Mt. St. Patrick. Those plants growing on the north-western face were fully exposed to the prevailing wind from that direction, which was seen to be blowing at gale force on a number of occasions. The far side of the peak was sheltered from the full effect of this for the most part, and was therefore usually significantly warmer under such conditions. On the other hand, personal experience elsewhere in the mountains suggests that the winters snow would lie for a significantly longer period on the sheltered southern slope than that on the northern side during the spring thaw. Both of these factors could have significant effects on the environmental triggers that control the timing of anthesis in one or other, or both, of the populations, possibly delaying the onset of flowering by a matter of weeks (Rathcke & Lacey 1985).

2.4.3 Preservation of Material and Herbarium Specimens

Specimens were prepared for storage in the Herbarium by air-drying, rather than pressing and mounting. This was for purely practical reasons, particularly in the case of the pulvinate specimens, which were simply too rigid of form to be pressed.

This method seemed to work well, with little structural damage to the vegetative parts. However, the individual florets showed a tendency to come loose from the receptacle, as is their purpose, during drying. Any florets or achenes that did so were retrieved and retained with the specimen.

2.4.4 Preparation of Organ Sections

Organ specimens were embedded in resin rather than wax as this medium was deemed to be faster to prepare and utilise, and also more efficient in terms of space and materials used. Despite this, preparation of slides was still a process that could easily take days to complete.

In order to keep slide numbers to a minimum, only two specimens from each population were investigated. For this reason, only qualitative anatomical characters were employed in the analysis. Confirmation of the constancy these characters could be confirmed in other specimens by simply taking a hand section and examining it under a light microscope. Quantitative characters, such as cell dimensions, could not be measured accurately using this quick method, and so were merely noted, or expressed as comparative data.

3 Characters and Analysis

3.1 Vegetative Morphology

Vegetative characters were divided into the groups of habit and leaf morphology. Habit features included those recorded in the field when the specimen was collected, or those that could be measured simply by looking at the specimen in the lab. Characters relating to leaf morphology could usually only be measured accurately once the leaf had been dissected out from the preserved specimen, shaved of the obscuring hairs, and examined under the dissecting microscope. All features that showed variance within a single specimen were measured from four different leaves, and the average taken (rounded to a single decimal point).

In this discussion, the term 'lamina' refers to the photosynthetic surface of the leaf, generally thickened and covered by a reticulate network of veins. The 'sheath' refers to the thinner, non-photosynthetic lower part of the leaf, through which only a few major vessels run. The interface between the two is usually well demarcated.

3.1.1 Habit characters

- Growth form: (1) sprawling, (2) decumbent, (3) rhizomatous, (4) pulvinate.

'Sprawling' here refers to a number of long lateral shoots trailing across the substrate, with no differentiation in structure between the primary and secondary branches. A 'decumbent' plant is one in which the secondary branches are upturned or erect. 'Rhizomatous' is similar to 'decumbent', except that the primary stems run

beneath the substrate and the secondary branches appear as a number of erect shoots scattered across the scree. 'Pulvinate' refers to the cushion form, in which a solid exterior surface is presented to the environment.

- Height of plant: (1) up to 100mm, (2) reaching more than 100mm.

This refers to the maximum height of the plant perpendicular to the axis of the substrate. Approximate measurements, rather than specific figures, were recorded due to the difficulties in obtaining accurate measurements in a number of specimens.

- Ultimate branchlets: (1) lax, (2) loosely packed, (3) densely packed.

If the branchlets are lax, there is no order or structure in their arrangement, other than that imposed by the form of the substrate. Branchlets that are loosely packed are generally of approximately the same length and grow close together, but are easily displaced. Densely packed branchlets are of the same length and appressed to one another, such that a solid face is presented.

- Secondary thickening of the stem: (1) little or none, (2) moderate.

This character refers to the main stem or stems. Measurements were not taken from rhizomes.

- Leaf apices: (1) distinguishable, (2) non-distinguishable.

The distinctness of the leaf apices in pulvinate plants is a function of the length and density of the obscuring leaf hairs. When viewed from the top, the apices of the appressed leaves surrounding the branchlet are visible if the leaf hairs are short or

sparse. Otherwise, the branchlet end appears to be a single structure, with only the terminal leaf buds visible at the centre.

If the growth form is non-pulvinate, this character is not applicable. Only in the pulvinate specimens are the leaves so closely appressed that the character may be measured.

- Leaf colour: (1) yellow, (2) yellow-green, (3) green, (4) grey.

Leaf colour was determined before the leaf hairs were removed, as these often contribute a large percentage of the plant's apparent colour.

3.1.2 Leaf position and morphology

- Angle between lamina apex and stem axis: (1) less than 35°, (2) 35° up to 45°, (3) 45° up to 90°, (4) 90° or more.

- Angle between lamina base and stem axis: (1) less than 35°, (2) 35° up to 45°, (3) 45° up to 90°, (4) 90° or more.

Measurements were taken between the leaf node and the furthest extremity of the lamina and the centre-point of the sheath/lamina interface respectively (figure 3.1). These characters are measured in order that, when studied in conjunction with respective lengths of the lamina (a) and the sheath (b), the degree of recurvature in the leaf can be calculated. The formula for this calculation is

$$\delta = 180 - (\alpha + \sin^{-1}(b / (a / \sin \alpha)))$$

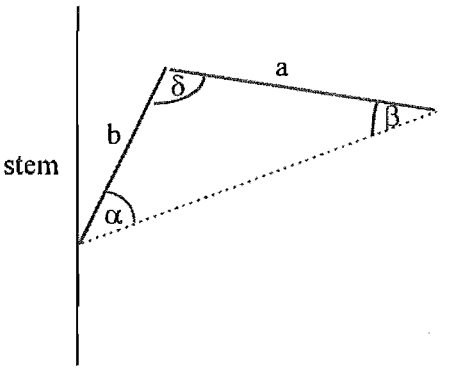


Fig 3.1: Diagram of the geometric relationship between the angle of lamina recurvature and the stem axis in *Haastia*.

where δ is the angle of recurvature, and α is the difference between the two measured angles. The latter part of the formula deals with the calculation of the third angle, β.

- Internode length: (1) not discernible, (2) always less than 1mm, (3) reaching more than 1mm.

The distance between leaf nodes on the stem axis was measured between mature, functional, healthy leaves that showed no sign of senescence. Maximum distances rather than absolute values were recorded due to the difficulties of achieving accurate measurements. A 'not discernible' result refers to a negligible record, rather than to a result that was not obtainable.

- Lamina length: mm
- Sheath length: mm

These were recorded as absolute values, and form two elements of the calculation of the angle of leaf recurvature (see above). Each was measured along the vertical axis of the leaf.

- Ratio of sheath length to lamina length.
- Ratio of lamina breadth to lamina length.
- Ratio of sheath breadth to lamina length..

The lamina breadth was measured at the widest point. The sheath breadth was measured near the interface of sheath and lamina, at the point where the leaf begins to widen.

When these measurements are interpreted in conjunction with one another, it is possible to describe the shape of the leaf. For this reason, observations of the leaf shape are not included in the analysis as a discrete measurement, in order to avoid repetition. They will, however, be included in the discussion of results.

- Leaf apex shape: (1) obtuse, (2) truncate, (3) rounded.

The criteria for the shape of the leaf apex follow those outlined by Dilcher (1974). An 'obtuse' leaf apex is one which meets at a point, the angle of which is greater than 90°. A 'truncate' apex is flattened, and does not form a point at all, while a 'rounded' apex forms a smooth arc.

- Lamina surface: (1) crenellate, (2) bullate, (3) rugose.

This applies to the ventral surface of the lamina. 'Crenellate' refers to fleshy projections of tissue covering the surface, particularly along the margin. A 'bullate' leaf has a surface which bulges significantly between the veins of the lamina. 'Rugose' is applied where the lamina surface does not bulge, but the pattern of venation is traced with wrinkles, producing the effect of lumpiness.

- Number of major nerves: (1) 3, (2) < 5, (3) < 10

The number of veins running through the sheath is either uniform throughout the population, with only three nerves visible, or variable. In the latter case, the number may vary between three and five, or around six to eight, up to a maximum of ten.

- Marginal downturn: (1) marked, (2) moderate, (3) little or none.

On a number of specimens, the margin of the lamina shows a tendency to fold under itself. While difficult to measure with an exact value, this can be estimated visually as 'little or none' (less than 10°), 'moderate' (10°-45°), and 'high' (45°-90°).

- Marginal sinuses: (1) mainly longer than wide, (2) mainly wider than long, (3) negligible.

Due to the variation in the size of the marginal crenallations on a single lamina, this was also difficult to accurately measure. 'Negligible' applies here when the depths of the marginal sinuses are less than $1/8^{th}$ of the intervening distance between any two.

3.2 Floral Morphology

Only approximately half of the specimens collected were actually carrying floral material, so this data matrix was necessarily restricted in comparison to the vegetative matrix. In addition, the condition of the floral material collected was dependent upon the date of collection; florets began to deteriorate rapidly soon after the completion of fertilisation. Floral material collected after mid-February was often too degraded to dissect and measure, while floral material collected before

mid-December usually consisted only of the phyllaries of the previous years capitula.

Much of the supplemental material gathered during the second summer of the project was used to provide enough data for a significant result to be reached. This applied particularly to the capitula of *Haastia recurva*, which were seriously damaged by insect predators nearly three times as often as those of the other taxa.

Floral characters were divided into those relating to the arrangement and structure of the capitula, and those relating to the structure of the individual florets. Capitulum characters could be measured by the naked eye, or under low magnification using the light microscope. Floret characters required investigation under the light microscope, or under the Scanning Electron Microscope (SEM).

- Position of capitula: (1) sessile, (2) elevated

Sessile capitula are located on the surface of the main body of the plant, in many cases half hidden by the foliage with only the top of the disc visible. Elevated capitula are borne on branches that have significantly elongated internodes in comparison to the vegetative branches (although leaf numbers remain similar), such that the inflorescence may be up to 2cm above the foliage, in a more exposed position.

- Capitulum diameter: mm
- Involucral bract length: mm

The diameter of the capitulum was measured across the receptacle at the base of the inflorescence, and the involucral bract length measured along the central axis on the inner face.

- Ratio of female florets to hermaphrodite florets.

As is common amongst the Compositae, the inner disc florets are functionally hermaphrodite, while the outer florets are reduced in structure, and are functionally and structurally female.

- Ratio of involucral bract length to hermaphrodite floret length.
- Ratio of female floret length to hermaphrodite floret length.
- Ratio of pappus hair length to hermaphrodite floret length.

Floret length was measured from the base of the achene to the apex of the corolla. Pappus hairs were measured from the collar of the achene.

- Ratio of breadth to length in the involucral bracts.

Bract breadth was measured at the widest point of the bract, or half way along the bract length.

- Involucral bract shape: (1) linear, (2) elliptic, (3) ovate, (4) obovate.

Bract shape is dependent on the position of the widest point. If the bract is of uniform breadth along its length, it is recorded as 'linear'. An 'elliptic' bract is widest in the middle, while 'ovate' and 'obovate' bracts are widest in the lower and upper parts of the bract respectively.

- Bract apex shape: (1) acute, (2) apiculate.

An 'acute' bract apex tapers evenly, while one that is 'apiculate' widens significantly at shoulders just below the apex.

- Number of veins in the bract: (1) one, (2) two.

This refers only to major nerves in the bract.

- Branching of veins in the bract: (1) no, (2) yes.

If branching of the bract veins is observed, it consists of the formation of two to five secondary veins.

- Senesence in bract apices: (1) high, (2) low.

If senesence in the bracts is apparent, the cells begin to die back from the bract apex early in the flowering season.

- Ratio of anther length to hermaphrodite floret length.

The cylindrical anthers are bipartite and are fused to the filament for almost their entire length.

- Style arm apices of hermaphrodite florets: (a) papillose, (b) caespitose.

If the apices of the style arms are 'papillose', the papilli are short and uniformly distributed. If they are observed to be 'caespitose', the papilli are longer and form tufts on the apex.

- Pappus hairs: (a) united, (b) free

The pappus hairs are 'united' (connate) if they are fused to one another at the base, where they are attached to the collar of the achene. They are scored as 'free' if each hair is individually attached to the achene.

3.3 Leaf Anatomy

- Abaxial epidermal cell size: (1) uniform, (2) not uniform.
- Adaxial epidermal cell size: (1) uniform, (2) not uniform.

Cells were considered 'not uniform' only if there was significant variation in cell area.

- Epidermal cell shape: (1) mainly wider than high, (2) mainly higher than wide.

Cell shape was scored according to an assessment of the majority of cells, as both forms could be often found within any suite of cells.

- Abaxial epidermal cells around veins and/or ribs, compared to abaxial epidermal cells elsewhere: (1) smaller, (2) equal size, (3) larger.

The abaxial epidermal cells associated with the major veins of the leaf often differ in size from the other abaxial cells. As above, significant size differences were required for other than 'equal size' to be recorded.

- Palisade cell layers: (1) one, (2) more than one.

'More than one' was recorded if a significant number of palisade cells were observed to be significantly out of alignment with the main axis of the palisade layer. This second 'layer' did not necessarily need to be complete.

- Palisade cell arrangement: (1) densely packed, (2) not densely packed.

The palisade cell arrangement was scored as being 'densely packed' if individual palisade cells were closely aligned, with little or no space between. Otherwise, 'not densely packed' was recorded.

- Position of palisade cells: (1) abaxial, (2) adaxial, (3) both abaxial and adaxial.

The position of the palisade layer(s) was scored according to the surface immediately adjacent, i.e. with no mesophyll cells intervening.

- Palisade cell distribution across lamina: (1) uniform, (2) not uniform.

Distribution of the palisade cells across the lamina was deemed 'not uniform' if any significant gaps in the palisade layer were noted on a slide, or if palisade cells were not seen on both the slides of the central part of the lamina, and of the apex region.

- Mesophyll cell size: (1) uniform, (2) not uniform.

As with the epidermal cells, significant size differences between the individual cells were required for a record of 'not uniform' to be made.

- Mesophyll cell shape: (1) mainly wider than high, (2) mainly higher than wide, (3) mainly equal dimensions.

Only the state of the majority of cells was recorded, for reasons similar to those of the shape of the epidermal cells.

- Resin canals: (1) present, (2) absent.

If canals were noted as 'present' they were seen to be associated with the vascular bundles of the lamina and sheath.

3.4 Rejected Characters

A number of characters were considered for inclusion in the analysis, but were rejected for one reason or another. These included characters that are synonymous with, or closely linked to, one or more of the characters listed above, characters that are strongly influenced by external factors, and characters that simply could not be measured given the time and resource limitations of this project. Despite their non-inclusion in the analysis, however, the states of several of these characters, particularly those common to all taxa, will be noted in the results.

3.5 Analysis of data

3.5.1 Methods

The characters outlined above were selected, measured and analysed following the techniques of numerical phenetic taxonomy. All the available data was scored for every specimen collected and recorded in a data matrix compiled using Microsoft Excel. For the sake of simplicity and ease of manipulation, the average value (for continuous characters) or the mode (for features measured in discrete values) was then taken for every character measured in each population, and used for the remainder of the analysis. Despite this precaution, some character values, particularly those pertaining to floral morphology, remained undetermined through non-availability for a small number of populations.

Characters fell into one of three types for the purposes of analysis; continuous, multi-state ordered, and multi-state unordered. The criteria for each character type is best illustrated in the following table.

Character type	Discrete character states?	Gradient of values applicable?
Continuous	no	yes
Multi-state Ordered	yes	yes
Multi-state Unordered	yes	no

Table 3.1: Criteria for the assignment of character types for numerical phenetic analysis.

Discrete character states generally have a obvious discontinuity separating one from the other, and are easily defined. Continuous characters show no such separation between the states, and are measured as absolute values.

The resultant data was then applied to one of two equations, depending upon the character type. For continuous and ordered characters, Gower's General Coefficient of Similarity (Gower 1971) was utilised. This may be simply expressed as the following formula:

$$S_{ijk} = 1 - ((x_i - x_j)/R_k)$$

This equation cannot be applied to unordered or qualitative characters, and so the Simple Matching Coefficient (Gower 1971) is instead applied in these instances:

$$\text{if } x_i = x_j, \text{ then } S_{ijk} = 1$$

$$\text{if } x_i \neq x_j, \text{ then } S_{ijk} = 0$$

In both formulas, 'S' is the standardised similarity (a value no less than zero and no greater than one), 'i' is the first OTU (Operational Taxonomic Unit, in this case representing a population), 'j' is the comparative OTU (another population), 'k' is

the character in question, 'x' is the state of that character in each OTU, and 'R' is the total range of that character in the sample tested (Gower 1971).

Using these equations, the standardised similarity was calculated for each character of every pair of OTUs. This data was then totalled for each pair, so that the overall similarity between any two populations was calculated, and recorded in a triangular matrix.

A dendrogram was created from the overall similarities by linking the OTUs according to the arithmetic average clustering method (Sneath & Sokal 1973: 228). This technique finds the average similarity between the members of any two OTUs, or clusters of OTUs, and links them at that point. In this way, the distortions of the two extreme methods of clustering, single linkage and complete linkage, are avoided in the dendrogram (Sneath & Sokal 1973: 228).

Other than the original measurement and scoring of the character states, the entire process was carried out using the statistical package, S-plus for Windows, on an IBM PC.

3.5.2 Discussion

The primary factor in the selection of a method of data analysis was objectivity. A technique was required that would minimise the degree of subjectivity in the analysis, one of the major sources of bias in taxonomic analyses in the past. The two methods of analysis that best fitted this criterion were the numerical phenetic

technique (following Sokal & Sneath 1963) and the cladistic technique (proposed by Hennig 1965), otherwise known as phylogenetic systematics or parsimony analysis. Both types of analysis make extensive use of statistical equations and formulae, thereby removing many of informal 'judgement calls' of traditional taxonomic techniques.

Of these two techniques, cladistic analysis was deemed unsuitable for application to this group. One of the requirements of this method of analysis is the polarisation of character states, categorising them as either plesiomorphic (primitive) or apomorphic (advanced) (Hennig 1965). The most efficient method of achieving this is by means of 'out group comparison', i.e. comparison of the characters with those of a group known to be closely related to the taxa under investigation (Stevens 1980). Where the out group is uncertain, as is the case with *Haastia*, then 'in group analysis' is possible, the most common character states within the group under investigation being taken as primitive. However, Stevens (1980) shows this method to be questionable, particularly when applied to small groups. In the absence of a reliable out group, it seemed safer not to use a cladistic analysis at this stage (see also Stuessy 1990: 103).

Numerical phenetics, on the other hand, does not take evolutionary lineage into account, and may easily be applied to groups of uncertain ancestry (Sokal & Sneath 1963: 216). The prominence of morphological similarity has been criticised in the past as not accounting for convergence of separate evolutionary lineages (e.g. Hennig 1966), but, in this case, the possibility of such convergence (also known as 'homoplasy') has been raised by Merxmüller *et al.* (1977), and is one of the issues

under investigation. Under these circumstances, such criticism does not necessarily apply, as evidence of convergence is being actively sought. Therefore, numerical phenetics was utilised as the primary method of analysis, although the resulting suggested classification was modified slightly by non-morphological factors, such as geographical and ecological distribution of taxa.

4 Results

4.1 Ecology and Distribution

All populations from which specimens were collected were situated in high alpine habitats; rocky, barren, often steep slopes, usually above 1500m (5000') of altitude, although one population of *H. recurva* (Poulter Hill) was seen to extend to as low as 1300m (4300') on a suitable scree slope. Within the parameters of this environment, *H. sinclairii* was found growing in a variety of habitats, including deep scree slopes, clay based fell fields, and in crevices on rocky outcrops. *H. sinclairii* was the only species that was found in numbers on the western side of the Main Divide, being collected from the Douglas Range in Northwest Nelson, from Scott Basin in Fiordland, and having been seen in the Otira Valley (pers. obs.) and at the headwaters of the Maruia River (Dr. D. Norton). *H. pulvinaris* and *H. recurva*, on the other hand, showed preference for the low rainfall regions of Marlborough, eastern Nelson, and North Canterbury. Both these species were found only on stable scree slopes or around the bases of outcrops. *H. recurva* showed a particular preference for deep screes, where it occurred in the greatest concentrations. Neither of these species was impaired in any way by wind exposure, and were often found growing on high ridges or summits, weathering the full force of the prevailing nor'-west wind. *H. sinclairii* was usually found on the more sheltered slopes, or in snow hollows.

None of the taxa were found consistently co-occurring with other forms of vegetation. Only on a few occasions was *H. pulvinaris* noted growing in association with tussocks, and then only in the lowest reaches of the habitat, or where a

particularly large specimen had stabilised the scree slope to the extent that grasses and herbs could colonise. The two forms of *H. pulvinaris* were frequently observed growing adjacent to one another (Fig 4.1), although *H. pulvinaris* var. *minor* usually occurs on the exposed rock outcrops rather than the scree slopes. The line of demarcation between populations of the two forms often follows a physical feature, such as a ridge top. The two varieties of *H. recurva* were not seen to co-occur, and neither were *H. sinclairii* and its southern form, var. *fulvida*. However, the populations of *H. sinclairii* and the 'Potts' form growing on Mt. Potts are found in the vicinity of one another.

Figure 4.1: *Haastia pulvinaris* var. *pulvinaris* (large plant) and *Haastia pulvinaris* var. *minor* co-occurring.

4.2 Morphology and Anatomy

4.2.1 Population Data

The populations listed in the following tables are coded according to taxon and site in the following manner. The first part of the code represents the taxon; genus and species, followed by variety or form if necessary. Thus 'Hs.' = *H. sinclairii*, 'Hsf.' = *H. sinclairii* var. *fulvida*, and 'HsP.' = *H. sinclairii* 'Potts'. Similarly, 'Hp.' = *H. pulvinaris*, 'Hpm.' = *H. pulvinaris* var. *minor*, 'Hr.' = *H. recurva*, and 'Hrw.' = *H. recurva* var. *wallii*.

The second part of the code represents the site. This is the first three letters of either the name of the mountain, or of the skifield. In this manner, 'Kak' = Kakapo Peak, 'Tap' = Tapu-ea-nuku, 'Fyf' = Mt. Fyffe, 'Sch' = Mt. Schiza, 'TeR' = Mt. Te Rako, 'Bar' = Barefell, 'Sou' = Mt. Southey, 'McC' = Mt. McCabe, 'Pri' = Mt. Princess, 'Bal' = Balaklava Ridge, 'StP' = Mt. St. Patrick, 'Edi' = Mt. Edison, 'PoR' = the Poulter Range, 'PoH' = Poulter Hill, 'Cra' = the Craigieburn Valley skifield, 'Bro' = the Broken River skifield, 'Hut' = Mt. Hutt, 'Pot' = Mt. Potts, 'Oha' = the Ohau skifield, and 'Bon' = Mt. Bonpland.

Population	Growth form				Ultimate branchlets		
	sprawl	decumb.	rhizome.	pulv.	lax	loose	dense
Hs.Kak	✓				✓		
Hs.TeR			✓			✓	
Hs.Bar			✓			✓	
Hs.Sou			✓		✓		
Hs.PoR	✓				✓		
Hs.Cra		✓				✓	
Hs.Bro		✓				✓	
Hs.Hut			✓			✓	
Hs.Pot			✓		✓		
Hs.Oha	✓				✓		
Hsf.Bon	✓				✓		
HsP.Pot		✓			✓		
Hp.Tap				✓			✓
Hp.Fyf				✓			✓
Hp.TeR				✓			✓
Hp.Sch				✓			✓
Hp.McC				✓			✓
Hp.Pri				✓			✓
Hp.Bal				✓			✓
Hp.StP				✓			✓
Hpm.Tap				✓			✓
Hpm.Sch				✓			✓
Hpm.Pri				✓			✓
Hpm.StP				✓			✓
Hpm.Edi				✓			✓
Hr.Edi		✓			✓		
Hr.PoH		✓				✓	
Hr.Cra	✓				✓		
Hr.Bro		✓				✓	
Hr.Hut		✓				✓	
Hrw.Sch		✓				✓	

Table 4.1 (a). Vegetative character states in sampled populations of *Haastia*: growth form, and density of the ultimate branchlets.

Population	Height of plant		Leaf apices		Internode length		
	<100mm	>100mm	disting.	obscure	not discern.	<1mm	<>1mm
Hs.Kak	✓						✓
Hs.TeR		✓					✓
Hs.Bar	✓						✓
Hs.Sou	✓					✓	
Hs.PoR	✓					✓	
Hs.Cra	✓					✓	
Hs.Bro		✓				✓	
Hs.Hut	✓				✓		
Hs.Pot	✓						✓
Hs.Oha	✓						✓
Hsf.Bon		✓					✓
HsP.Pot	✓						✓
Hp.Tap		✓	✓		✓		
Hp.Fyf	✓		✓		✓		
Hp.TeR	✓		✓		✓		
Hp.Sch		✓	✓		✓		
Hp.McC		✓	✓		✓		
Hp.Pri		✓	✓		✓		
Hp.Bal	✓		✓		✓		
Hp.StP	✓		✓		✓		
Hpm.Tap		✓		✓	✓		
Hpm.Sch		✓		✓	✓		
Hpm.Pri		✓		✓	✓		
Hpm.StP		✓		✓	✓		
Hpm.Edi		✓		✓	✓		
Hr.Edi		✓			✓		
Hr.PoH		✓				✓	
Hr.Cra	✓						✓
Hr.Bro		✓					✓
Hr.Hut	✓					✓	
Hrw.Sch	✓					✓	

Table 4.1 (b). Vegetative character states in sampled populations of *Haastia*: average plant height, leaf apex appearance, and internode length.

Population	2° thick. of stem		Leaf colour				
	little	moderate	yellow	yell. green	green	bronze	grey
Hs.Kak		✓					✓
Hs.TeR		✓					✓
Hs.Bar		✓					✓
Hs.Sou		✓					✓
Hs.PoR		✓					✓
Hs.Cra		✓					✓
Hs.Bro		✓					✓
Hs.Hut		✓					✓
Hs.Pot		✓					✓
Hs.Oha		✓					✓
Hsf.Bon		✓			✓		
HsP.Pot		✓			✓		
Hp.Tap		✓		✓			
Hp.Fyf		✓		✓			
Hp.TeR		✓		✓			
Hp.Sch		✓		✓			
Hp.McC		✓		✓			
Hp.Pri		✓		✓			
Hp.Bal		✓		✓			
Hp.StP		✓		✓			
Hpm.Tap		✓	✓				
Hpm.Sch		✓	✓				
Hpm.Pri		✓	✓				
Hpm.StP		✓	✓				
Hpm.Edi		✓	✓				
Hr.Edi		✓		✓			
Hr.PoH		✓				✓	✓
Hr.Cra		✓					✓
Hr.Bro		✓				✓	✓
Hr.Hut		✓					✓
Hrw.Sch	✓			✓			

Table 4.1 (c). Vegetative character states in sampled populations of *Haastia*: secondary thickening of the stem, and leaf colour.

Population	Lamina length (mm)	Sheath length (mm)	Angle of recurve(°)
Hs.Kak	8.67	12	24.92
Hs.TeR	11	12	23.75
Hs.Bar	9	9	12.00
Hs.Sou	9.33	9	26.60
Hs.PoR	10	10	45.95
Hs.Cra	13	11	53.88
Hs.Bro	7.5	10.25	48.16
Hs.Hut	9	8	46.53
Hs.Pot	12.75	12.25	45.14
Hs.Oha	13	12.5	40.88
Hsf.Bon	22.5	14	60.55
HsP.Pot	11.5	9.5	41.69
Hp.Tap	2.5	6	85.94
Hp.Fyf	2	4	86.44
Hp.TeR	2.67	4.33	48.09
Hp.Sch	2	6	55.44
Hp.McC	2	5.5	55.32
Hp.Pri	2.33	6.33	48.29
Hp.Bal	2.67	6	73.92
Hp.StP	2	5	85.98
Hpm.Tap	2	8.5	55.39
Hpm.Sch	2	11	82.76
Hpm.Pri	2.5	6	57.42
Hpm.StP	2	5	59.56
Hpm.Edi	3.75	7.75	68.29
Hr.Edi	4	7	72.70
Hr.PoH	6	7.33	36.59
Hr.Cra	7.67	9.33	65.45
Hr.Bro	6	9	53.77
Hr.Hut	7	8	65.60
Hrw.Sch	6.75	7.75	85.30

Table 4.1 (d). Vegetative character states in sampled populations of *Haastia*: leaf dimensions and angle of lamina recurvature from the sheath axis.

Population	sheath lth.: lamina lth.	lamina wth.: lamina lth.	sheath wth.: lamina wth.
Hs.Kak	1.35	1.26	0.63
Hs.TeR	1.10	1.17	0.62
Hs.Bar	0.98	1.10	0.63
Hs.Sou	1.00	1.12	0.79
Hs.PoR	1.00	1.00	0.79
Hs.Cra	0.85	1.00	0.72
Hs.Bro	1.38	1.26	0.72
Hs.Hut	0.89	1.12	0.71
Hs.Pot	0.83	0.81	0.65
Hs.Oha	0.95	0.65	0.71
Hsf.Bon	0.66	0.55	0.44
HsP.Pot	0.83	0.85	0.65
Hp.Tap	2.45	2.69	0.78
Hp.Fyf	2.00	3.98	0.63
Hp.TeR	1.58	3.55	0.62
Hp.Sch	3.02	6.17	0.59
Hp.McC	2.75	4.27	0.65
Hp.Pri	2.69	3.55	0.65
Hp.Bal	2.29	3.89	0.71
Hp.StP	2.40	3.98	0.63
Hpm.Tap	4.17	3.16	0.83
Hpm.Sch	5.50	5.01	0.79
Hpm.Pri	2.40	2.82	0.71
Hpm.StP	2.51	3.47	0.85
Hpm.Edi	2.09	2.29	0.79
Hr.Edi	1.74	1.74	0.71
Hr.PoH	1.17	1.41	0.74
Hr.Cra	1.23	1.05	0.78
Hr.Bro	1.48	1.10	0.79
Hr.Hut	1.00	1.20	0.95
Hrw.Sch	1.15	1.07	0.79

Table 4.1 (e). Vegetative character states in sampled populations of *Haastia*: ratios of sheath length to lamina length, lamina width to lamina length, and sheath width to lamina width.

Population	Leaf apex shape			Lamina surface		
	obtuse	truncate	rounded	cren.	bullate	rugose
Hs.Kak	✓					✓
Hs.TeR			✓			✓
Hs.Bar	✓					✓
Hs.Sou	✓					✓
Hs.PoR	✓					✓
Hs.Cra	✓				✓	
Hs.Bro	✓				✓	
Hs.Hut	✓				✓	
Hs.Pot	✓					✓
Hs.Oha	✓					✓
Hsf.Bon			✓			✓
HsP.Pot			✓			✓
Hp.Tap		✓		✓		
Hp.Fyf		✓		✓		
Hp.TeR			✓	✓		
Hp.Sch			✓	✓		
Hp.McC			✓	✓		
Hp.Pri			✓	✓		
Hp.Bal			✓	✓		
Hp.StP			✓	✓		
Hpm.Tap		✓		✓		
Hpm.Sch		✓		✓		
Hpm.Pri		✓		✓		
Hpm.StP		✓		✓		
Hpm.Edi			✓	✓		
Hr.Edi			✓	✓		
Hr.PoH			✓		✓	
Hr.Cra	✓				✓	
Hr.Bro			✓		✓	
Hr.Hut	✓				✓	
Hrw.Sch	✓				✓	

Table 4.1 (f). Vegetative character states in sampled populations of *Haastia*: leaf apex shape and the quality of the upper surface of the lamina.

Population	Number of major nerves			Marginal inrolling			Marginal sinuses		
	3	< 5	< 10	low	mod.	high	deep	shallow	neg.
Hs.Kak		✓		✓					✓
Hs.TeR		✓		✓					✓
Hs.Bar		✓		✓					✓
Hs.Sou		✓		✓					✓
Hs.PoR			✓	✓					✓
Hs.Cra			✓	✓				✓	
Hs.Bro			✓		✓			✓	
Hs.Hut			✓		✓			✓	
Hs.Pot		✓		✓				✓	
Hs.Oha		✓		✓					✓
Hsf.Bon			✓	✓					✓
HsP.Pot		✓		✓					✓
Hp.Tap		✓			✓		✓		
Hp.Fyf		✓				✓		✓	
Hp.TeR		✓			✓			✓	
Hp.Sch		✓			✓			✓	
Hp.McC		✓			✓			✓	
Hp.Pri		✓			✓			✓	
Hp.Bal		✓			✓		✓		
Hp.StP		✓			✓		✓		
Hpm.Tap	✓				✓		✓		
Hpm.Sch	✓				✓		✓		
Hpm.Pri	✓				✓		✓		
Hpm.StP	✓					✓	✓		
Hpm.Edi	✓				✓		✓		
Hr.Edi	✓					✓	✓		
Hr.PoH	✓					✓		✓	
Hr.Cra	✓				✓			✓	
Hr.Bro	✓				✓			✓	
Hr.Hut	✓					✓		✓	
Hrw.Sch	✓					✓		✓	

Table 4.1 (g) Vegetative character states in sampled populations of *Haastia*: the number of major nerves, degree of marginal inrolling, and sinus depth.

Population	Capitulum position		Receptacle	Bract length	Bract length:	No. bract veins	
	sessile	elevated	diam. (mm)	(mm)	bract width	1	2
Hs.Kak							
Hs.TeR	✓		15	18	18.00		✓
Hs.Bar	✓		11	14	14.74		✓
Hs.Sou	✓		7	9	12.86	✓	
Hs.PoR							
Hs.Cra	✓		8	12	15.00	✓	
Hs.Bro	✓		7	11	12.94	✓	
Hs.Hut	✓		7	10	15.38	✓	
Hs.Pot	✓		6	11	18.33	✓	
Hs.Oha	✓						
Hsf.Bon	✓		9.5	9.5	7.92		✓
HsP.Pot		✓	8	9	8.18	✓	
Hp.Tap	✓		5	7	7.00		✓
Hp.Fyf	✓		6	6	7.06		✓
Hp.TeR	✓		5	7	8.75		✓
Hp.Sch	✓		6	6.5	9.29		✓
Hp.McC	✓		5.33	7	10.00		✓
Hp.Pri	✓		6.33	7.33	10.47		✓
Hp.Bal	✓		6	8	8.42		✓
Hp.StP	✓		4	5	7.14		✓
Hpm.Tap	✓		5	6	6.67		✓
Hpm.Sch	✓		5	6.5	7.65		✓
Hpm.Pri	✓		4.5	7	6.92		✓
Hpm.StP	✓		6	7	8.24		✓
Hpm.Edi	✓		4	7	8.75		✓
Hr.Edi	✓		9	11	11.00	✓	
Hr.PoH	✓		7.5	9.5	11.88	✓	
Hr.Cra	✓		8	9.5	10.56	✓	
Hr.Bro	✓		9	10	11.76	✓	
Hr.Hut	✓		7	9.25	10.88	✓	
Hrw.Sch	✓		6	9	11.25	✓	

Table 4.2 (a). Floral character states in sampled populations of *Haastia*: the bearing of the capitula, the receptacle width, the involucral bract length, the ratio of bract length to bract width, and the number of veins per bract.

Population	Bract shape				Branching of veins		Bract apex shape		Apex senesence	
	linear	elliptic	obovate	ovate	no	yes	acute	apic.	high	low
Hs.Kak										
Hs.TeR	✓				✓			✓	✓	
Hs.Bar	✓				✓				✓	
Hs.Sou	✓				✓		✓		✓	
Hs.PoR										
Hs.Cra	✓				✓		✓		✓	
Hs.Bro	✓				✓		✓		✓	
Hs.Hut	✓				✓		✓		✓	
Hs.Pot	✓				✓		✓		✓	
Hs.Oha										
Hsf.Bon	✓				✓		✓		✓	
HsP.Pot		✓				✓	✓		✓	
Hp.Tap				✓	✓		✓			✓
Hp.Fyf				✓	✓		✓			✓
Hp.TeR				✓	✓		✓			✓
Hp.Sch				✓	✓		✓			✓
Hp.McC				✓	✓		✓			✓
Hp.Pri				✓	✓		✓			✓
Hp.Bal				✓	✓		✓			✓
Hp.StP				✓	✓		✓			✓
Hpm.Tap			✓		✓		✓			✓
Hpm.Sch			✓		✓		✓			✓
Hpm.Pri			✓		✓		✓			✓
Hpm.StP			✓		✓		✓			✓
Hpm.Edi			✓		✓		✓			✓
Hr.Edi	✓					✓	✓		✓	
Hr.PoH	✓					✓	✓		✓	
Hr.Cra	✓					✓	✓		✓	
Hr.Bro	✓					✓	✓		✓	
Hr.Hut	✓					✓	✓		✓	
Hrw.Sch	✓				✓			✓	✓	

Table 4.2 (b). Floral character states in sampled populations of *Haastia*: the shape of the involucral bracts, branching patterns in the veins of the bracts, the shape of the bract apex, and the degree of senescence apparent in the bract apex.

Population	Fem. fl.: herm. fl.	Bract lth.: h. fl. lth.	F. fl. lth.: h. fl. lth.	Pap. lth.: h. fl. lth.	Style arm apices		Pappus hairs	
					papillose	caespitose	united	free
Hs.Kak								
Hs.TeR	0.75	1.18	0.67	1		✓		✓
Hs.Bar	0.63	1.27	0.59	1.81		✓		✓
Hs.Sou	0.68	2.25	0.29	1.51	✓			✓
Hs.PoR								
Hs.Cra	0.78	3.00	0.30	1.74	✓			✓
Hs.Bro	0.77	2.75	0.28	1.99	✓			✓
Hs.Hut	0.72	2.50	0.25	1.51	✓			✓
Hs.Pot	0.46	2.25	0.25	1.99	✓			✓
Hs.Oha								
Hsf.Bon	0.83	1.12	0.52	1.12	✓			✓
HsP.Pot	0.65	1.41	0.55	1.26	✓			✓
Hp.Tap	0.55	1.40	0.67	1.58		✓		✓
Hp.Fyf	0.53	1.00	0.75	1.66		✓		✓
Hp.TeR	0.69	1.17	0.69	1.51		✓		✓
Hp.Sch	0.65	1.08	0.71	1.38		✓		✓
Hp.McC	0.83	1.40	0.66	1.82		✓		✓
Hp.Pri	0.65	1.05	0.68	1.15		✓		✓
Hp.Bal	0.66	1.33	0.67	1.51		✓		✓
Hp.StP	0.73	0.83	0.73	1.32		✓		✓
Hpm.Tap	0.54	0.75	0.54	1.38	✓			✓
Hpm.Sch	0.54	0.93	0.56	1.35	✓			✓
Hpm.Pri	0.51	0.83	0.49	1.17	✓			✓
Hpm.StP	0.57	0.88	0.58	1.51	✓			✓
Hpm.Edi	0.48	0.88	0.58	1.51	✓			✓
Hr.Edi	0.89	2.00	0.25	1.26	✓		✓	
Hr.PoH	0.75	2.11	0.23	1.32	✓		✓	
Hr.Cra	0.79	2.71	0.25	1.86	✓		✓	
Hr.Bro	0.64	2.50	0.29	1.51	✓		✓	
Hr.Hut	0.74	2.31	0.27	1.51	✓		✓	
Hrw.Sch	0.70	1.75	0.30	1.17	✓		✓	

Table 4.2 (c). Floral character states in sampled populations of *Haastia*: ratios of numbers of female florets to hermaphrodite florets, bract length to hermaphrodite floret length, female floret length to hermaphrodite floret length, pappus hair length to hermaphrodite floret length, condition of the style arm apices, and the condition of the pappus hairs.

Population	Abaxial epi. dpth.: adaxial epi. dpth.			Abaxial epi. cell size		Adaxial epi. cell size	
	Greater	Less	Equal	uniform	not uniform	uniform	not uniform
Hs.Kak		✓			✓		✓
Hs.TeR		✓			✓		✓
Hs.Bar	✓				✓		✓
Hs.Sou			✓		✓		✓
Hs.PoR	✓				✓		✓
Hs.Cra			✓		✓		✓
Hs.Bro	✓				✓		✓
Hs.Hut			✓		✓		✓
Hs.Pot			✓		✓		✓
Hs.Oha			✓		✓		✓
Hsf.Bon			✓	✓		✓	
HsP.Pot		✓			✓		✓
Hp.Tap	✓				✓		✓
Hp.Fyf			✓		✓		✓
Hp.TeR			✓		✓		✓
Hp.Sch	✓				✓		✓
Hp.McC			✓		✓		✓
Hp.Pri			✓		✓		✓
Hp.Bal	✓				✓		✓
Hp.StP			✓		✓		✓
Hpm.Tap		✓			✓		✓
Hpm.Sch		✓			✓		✓
Hpm.Pri	✓				✓		✓
Hpm.StP		✓			✓		✓
Hpm.Edi		✓			✓		✓
Hr.Edi		✓			✓		✓
Hr.PoH		✓			✓		✓
Hr.Cra		✓			✓	✓	
Hr.Bro		✓			✓	✓	
Hr.Hut			✓		✓	✓	
Hrw.Sch		✓			✓	✓	

Table 4.3 (a). Anatomical character states in the leaves of sampled populations of *Haastia*: the depth of the abaxial epidermal cells in comparison to that of the adaxial epidermal cells, uniformity of abaxial epidermal cell size, and the uniformity of adaxial epidermal cell size.

Population	Epi. cell shape		Abaxial epi. cells assoc. veins.			Palisade layers.	
	wide>high	high>wide	smaller	equal	larger	single	>single
Hs.Kak	✓				✓		✓
Hs.TeR	✓				✓		✓
Hs.Bar	✓				✓		✓
Hs.Sou	✓				✓		✓
Hs.PoR	✓				✓		✓
Hs.Cra	✓				✓		✓
Hs.Bro	✓				✓		✓
Hs.Hut	✓				✓		✓
Hs.Pot	✓				✓		✓
Hs.Oha	✓				✓		✓
Hsf.Bon	✓			✓			✓
HsP.Pot	✓				✓		✓
Hp.Tap	✓			✓			✓
Hp.Fyf	✓			✓			✓
Hp.TeR	✓			✓			✓
Hp.Sch	✓			✓			✓
Hp.McC	✓			✓			✓
Hp.Pri	✓			✓			✓
Hp.Bal	✓			✓			✓
Hp.StP	✓			✓			✓
Hpm.Tap	✓			✓			✓
Hpm.Sch	✓			✓			✓
Hpm.Pri	✓			✓			✓
Hpm.StP	✓			✓			✓
Hpm.Edi	✓			✓			✓
Hr.Edi	✓		✓			✓	
Hr.PoH	✓				✓	✓	
Hr.Cra	✓				✓	✓	
Hr.Bro	✓				✓	✓	
Hr.Hut	✓				✓	✓	
Hrw.Sch	✓				✓		✓

Table 4.3 (b). Anatomical character states in the leaves of sampled populations of *Haastia*: epidermal cell shape, the size of the abaxial epidermal cells associated with the vascular bundle in comparison to other abaxial epidermal cells, the number of palisade cell layers.

Population	Palisade cell arrangement		Palisade layer position		Palisade cell dispersal	
	tight	loose	abaxial	adaxial	uniform	not uniform
Hs.Kak	✓			✓	✓	
Hs.TeR		✓		✓	✓	
Hs.Bar	✓			✓	✓	
Hs.Sou		✓		✓	✓	
Hs.PoR	✓			✓	✓	
Hs.Cra	✓			✓	✓	
Hs.Bro	✓			✓	✓	
Hs.Hut	✓			✓	✓	
Hs.Pot	✓			✓	✓	
Hs.Oha	✓			✓	✓	
Hsf.Bon	✓			✓	✓	
HsP.Pot	✓			✓	✓	
Hp.Tap		✓		✓		✓
Hp.Fyf		✓		✓		✓
Hp.TeR		✓		✓		✓
Hp.Sch		✓		✓		✓
Hp.McC		✓		✓		✓
Hp.Pri		✓		✓		✓
Hp.Bal		✓		✓		✓
Hp.StP		✓		✓		✓
Hpm.Tap	✓			✓		✓
Hpm.Sch	✓			✓		✓
Hpm.Pri	✓			✓		✓
Hpm.StP	✓			✓		✓
Hpm.Edi	✓			✓		✓
Hr.Edi	✓			✓	✓	
Hr.PoH		✓		✓	✓	
Hr.Cra		✓		✓	✓	
Hr.Bro		✓		✓	✓	
Hr.Hut		✓		✓	✓	
Hrw.Sch		✓		✓		✓

Table 4.3 (c). Anatomical character states in the leaves of sampled populations of *Haastia*: the arrangement of the palisade cells in relation to one another, the position of the palisade cell layer(s), and the dispersal of the palisade cell layer(s) across the leaf.

Population	Mesophyll cell size		Mesophyll cell shape		Vascular canals	
	uniform	not uniform	wide>high	high>wide	present	absent
Hs.Kak		✓	✓			✓
Hs.TeR		✓	✓			✓
Hs.Bar		✓	✓			✓
Hs.Sou		✓	✓			✓
Hs.PoR		✓	✓			✓
Hs.Cra		✓	✓			✓
Hs.Bro		✓	✓			✓
Hs.Hut		✓	✓			✓
Hs.Pot		✓	✓			✓
Hs.Oha		✓	✓			✓
Hsf.Bon	✓		✓			✓
HsP.Pot		✓	✓		✓	
Hp.Tap		✓	✓		✓	
Hp.Fyf		✓	✓		✓	
Hp.TeR		✓	✓		✓	
Hp.Sch		✓	✓		✓	
Hp.McC		✓	✓		✓	
Hp.Pri		✓	✓		✓	
Hp.Bal		✓	✓		✓	
Hp.StP		✓	✓		✓	
Hpm.Tap		✓	✓		✓	
Hpm.Sch		✓	✓		✓	
Hpm.Pri		✓	✓		✓	
Hpm.StP		✓	✓		✓	
Hpm.Edi		✓	✓		✓	
Hr.Edi		✓	✓			✓
Hr.PoH		✓	✓			✓
Hr.Cra		✓	✓			✓
Hr.Bro		✓	✓			✓
Hr.Hut		✓	✓			✓
Hrw.Sch		✓	✓			✓

Table 4.3 (d): Anatomical character states in the leaves of sampled populations of *Haastia*: the uniformity of size of the mesophyll cells, the shape of the mesophyll cells, and the presence of canals associated with the vascular tissue.

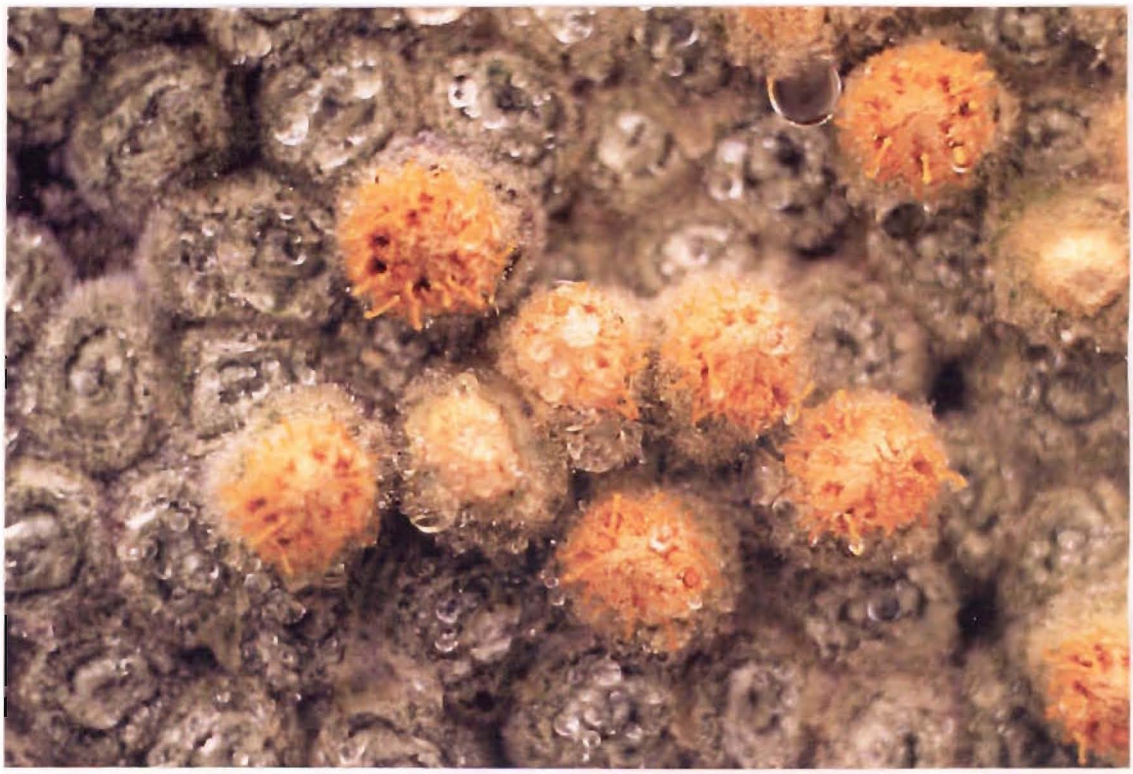
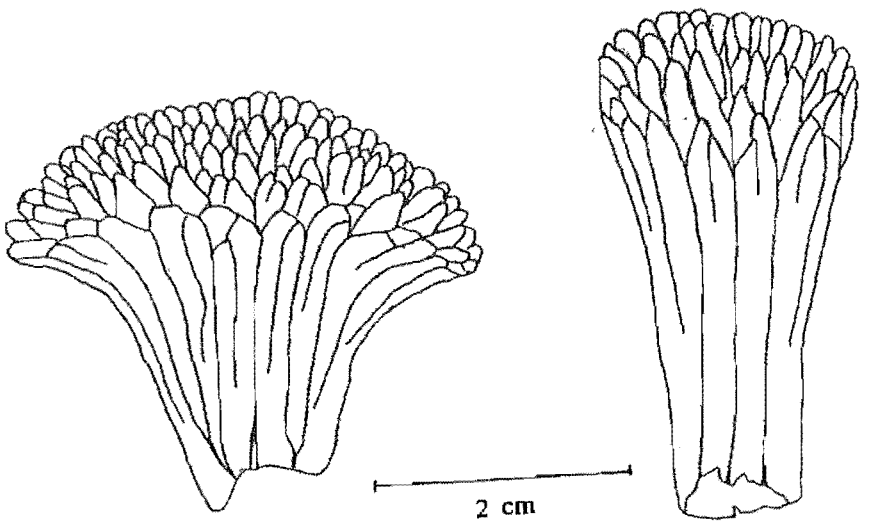


Figure 4.2: Detail of the branchlet tips of *Haastia pulvinaris* var. *pulvinaris*

Figure 4.3: Detail of the branchlet tips of *Haastia pulvinaris* var. *minor*.

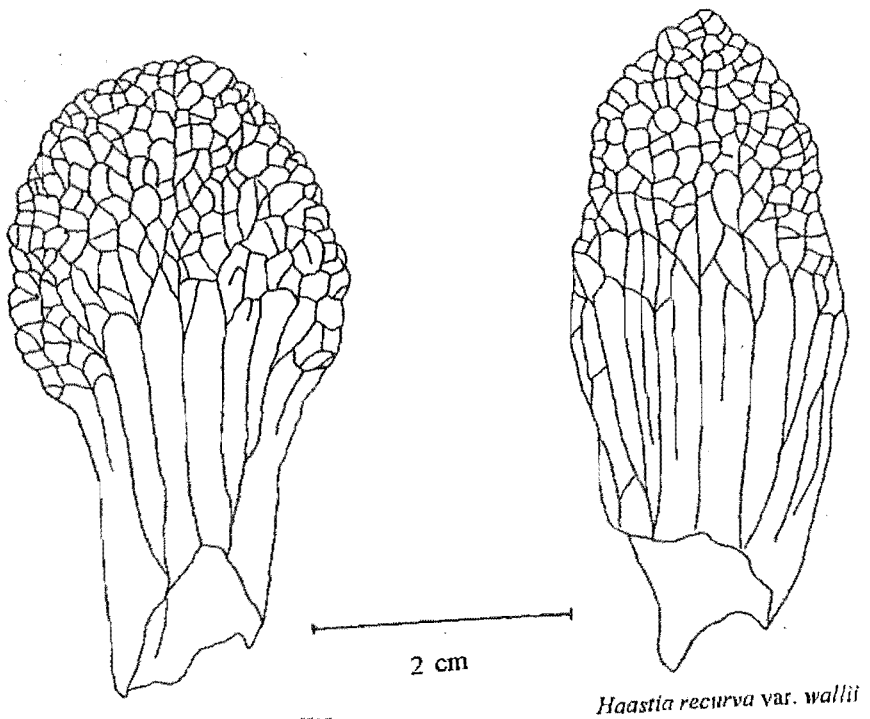


Haastia pulvinaris var. *pulvinaris*

(Balaklava Ridge)

Haastia pulvinaris var. *minor*

(Tapu-ea-nuku)



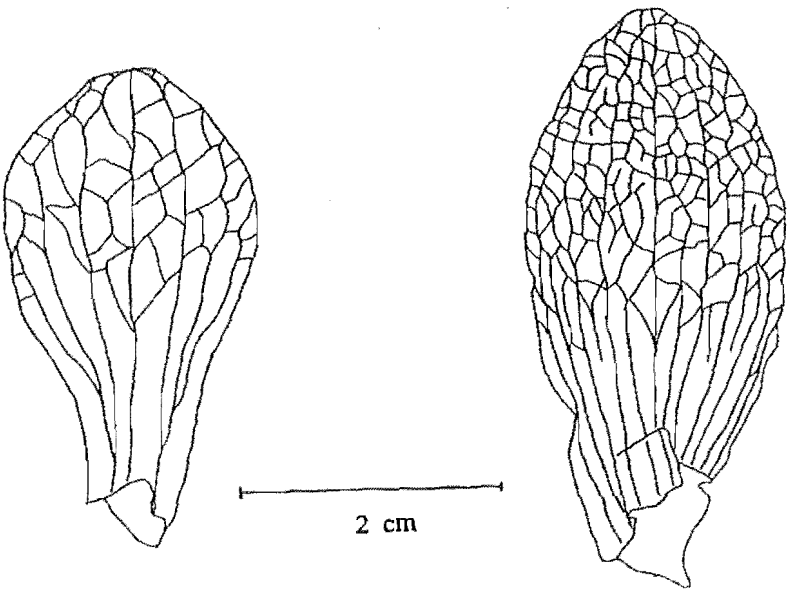
Haastia recurva var. *recurva*

(Poulter Hill)

Haastia recurva var. *wallii*

(Mt. Schiza)

Figure 4.4 (a): Leaf drawings of *Haastia* taxa.

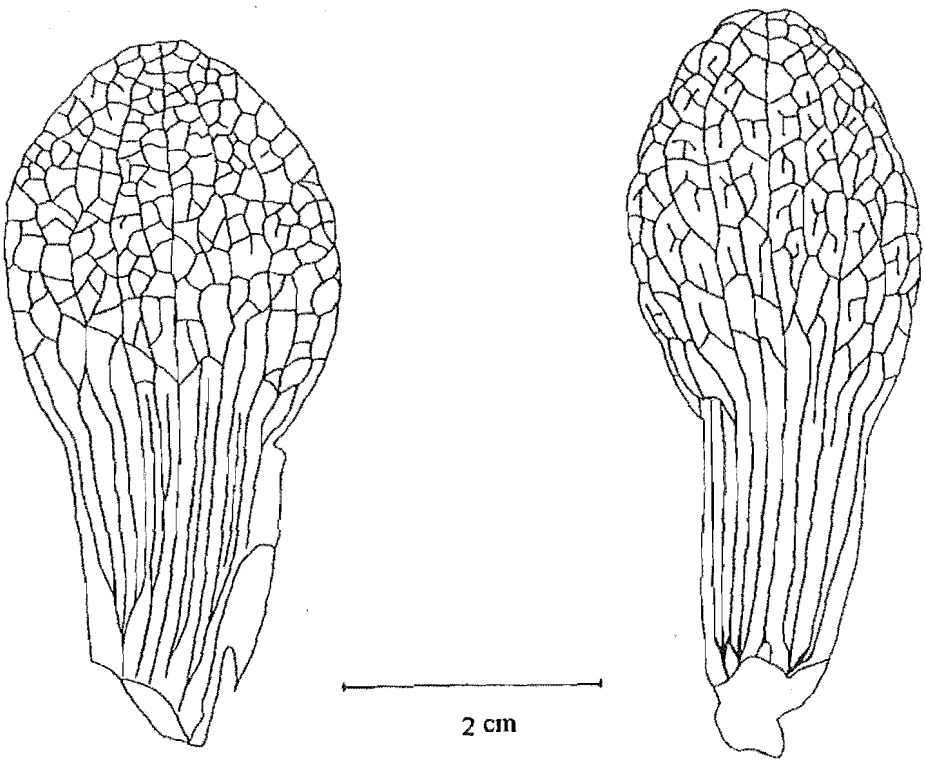


Haastia sinclairii var. *sinclairii*

(Kakapo Peak)

Haastia sinclairii 'Potts'

(Mt. Potts)



Haastia sinclairii var. *sinclairii* ?

(Mt. Te Rako)

Haastia sinclairii var. *fulvida*

(Mt. Bonpland)

Figure 4.4 (b): Leaf drawings of *Haastia* taxa (continued).

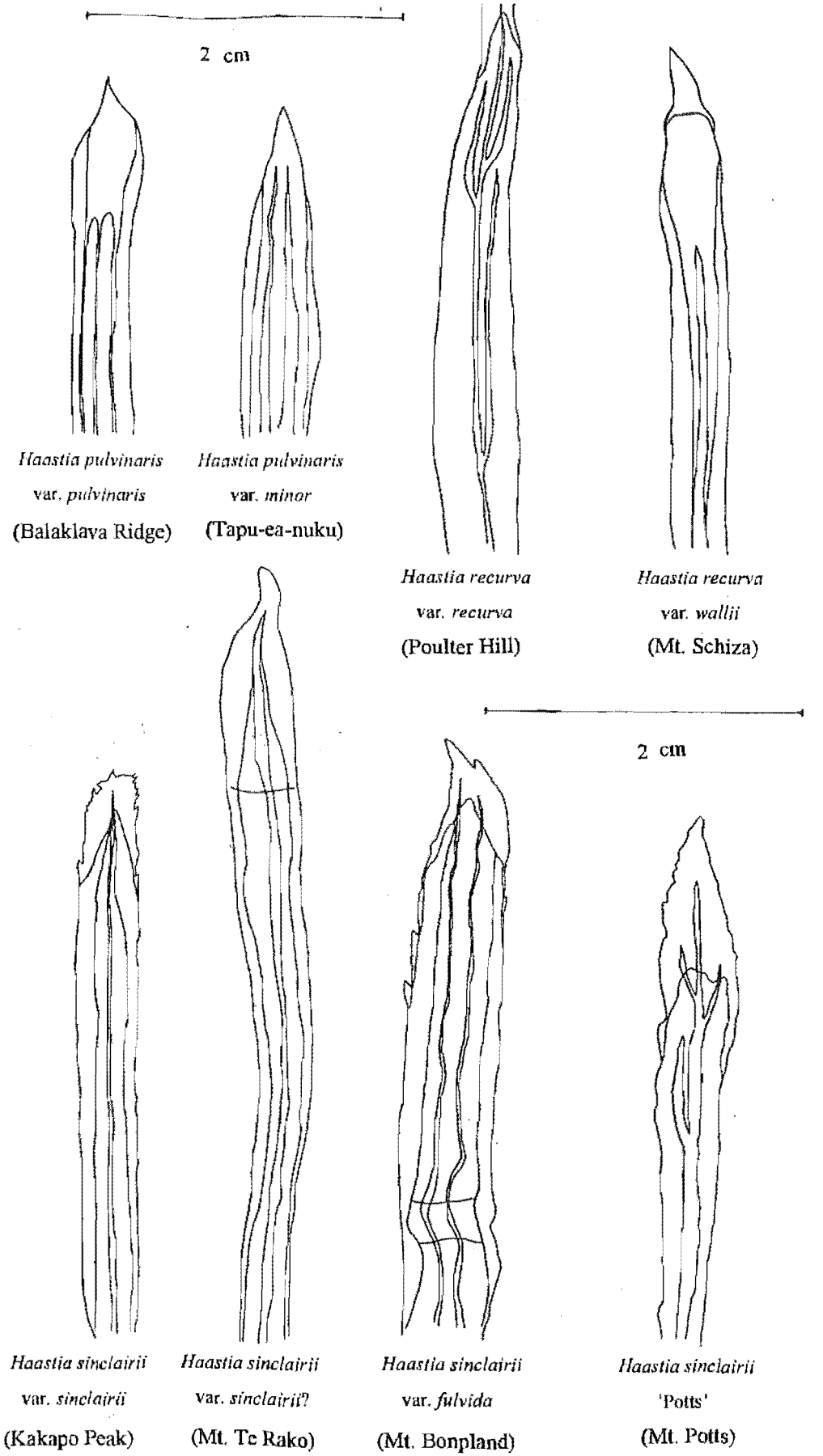


Figure 4.5: Involucral bract drawings of *Haastia* taxa

Figure 4.6: The form of *Haastia sinclairii* found at Mt. Terako.

Figure 4.7: Detail of the capitulum of the Mt. Terako form of *Haastia sinclairii*.

Figure 4.8: Detail of a floral stem with capitulum of *Haastia sinclairii* 'Potts'

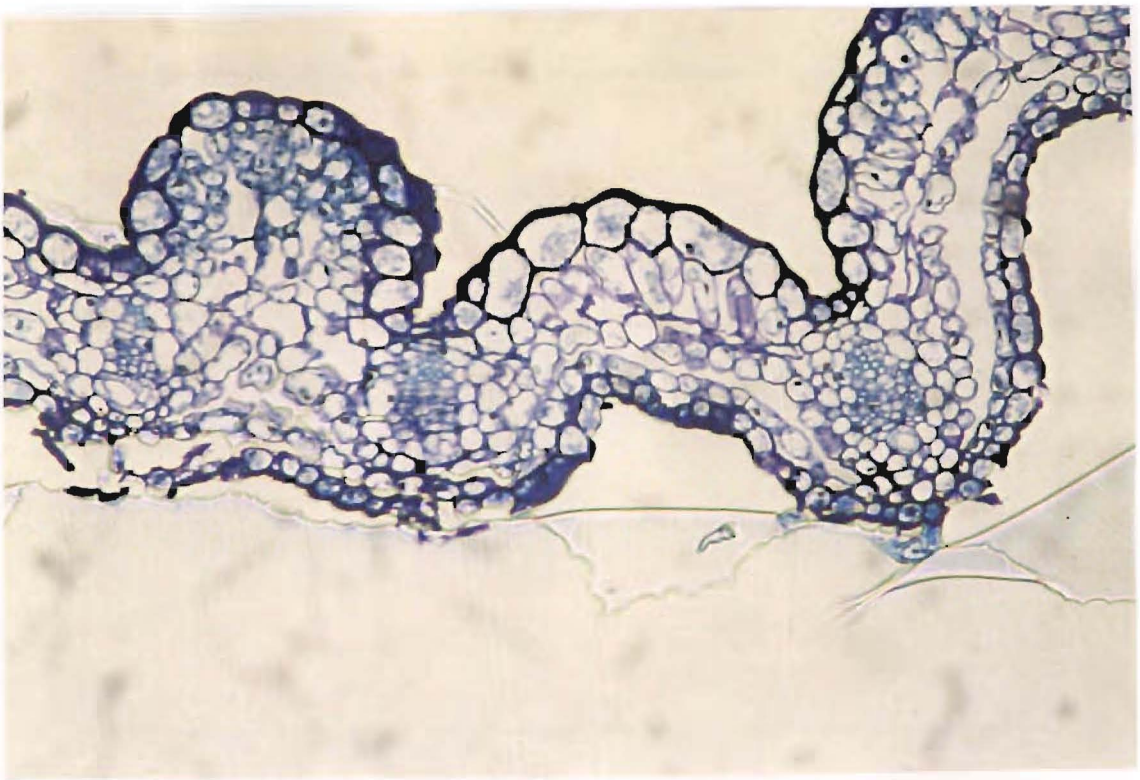


Figure 4.9: Anatomical leaf section of *Haastia pulvinaris* var. *pulvinaris*. 200 µ

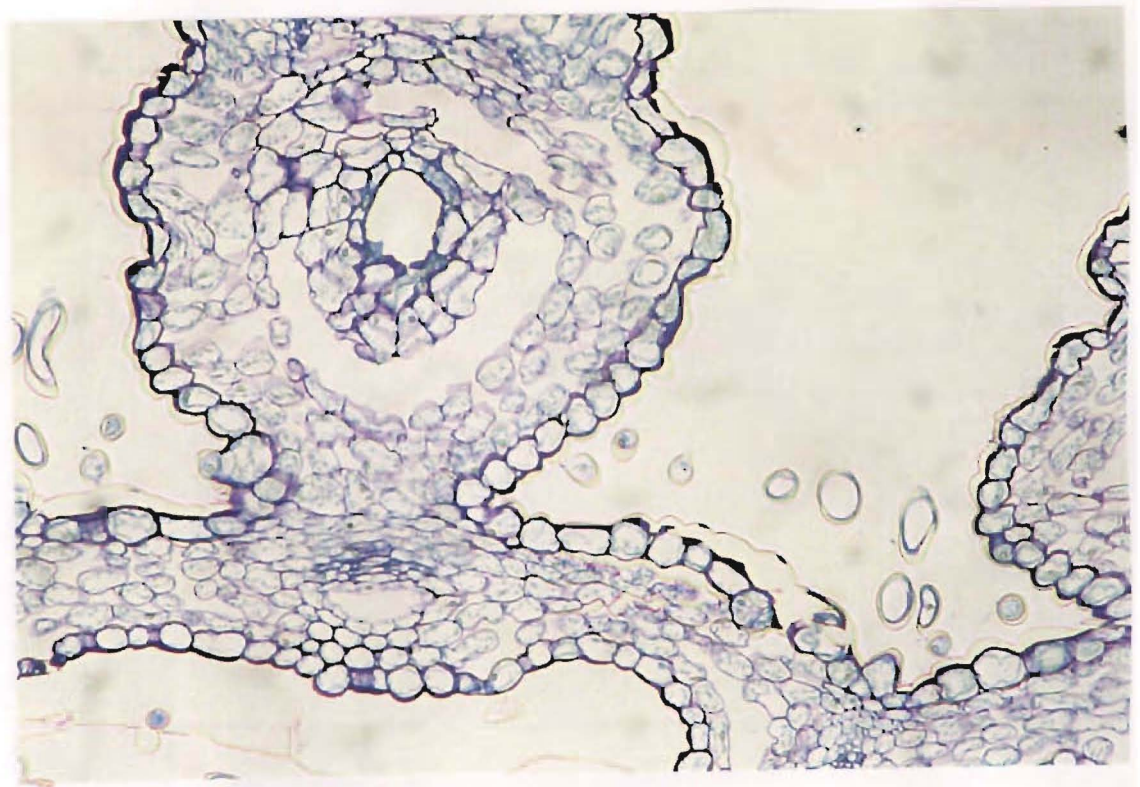


Figure 4.10: Anatomical leaf section of *Haastia pulvinaris* var. *minor*. 200 µ

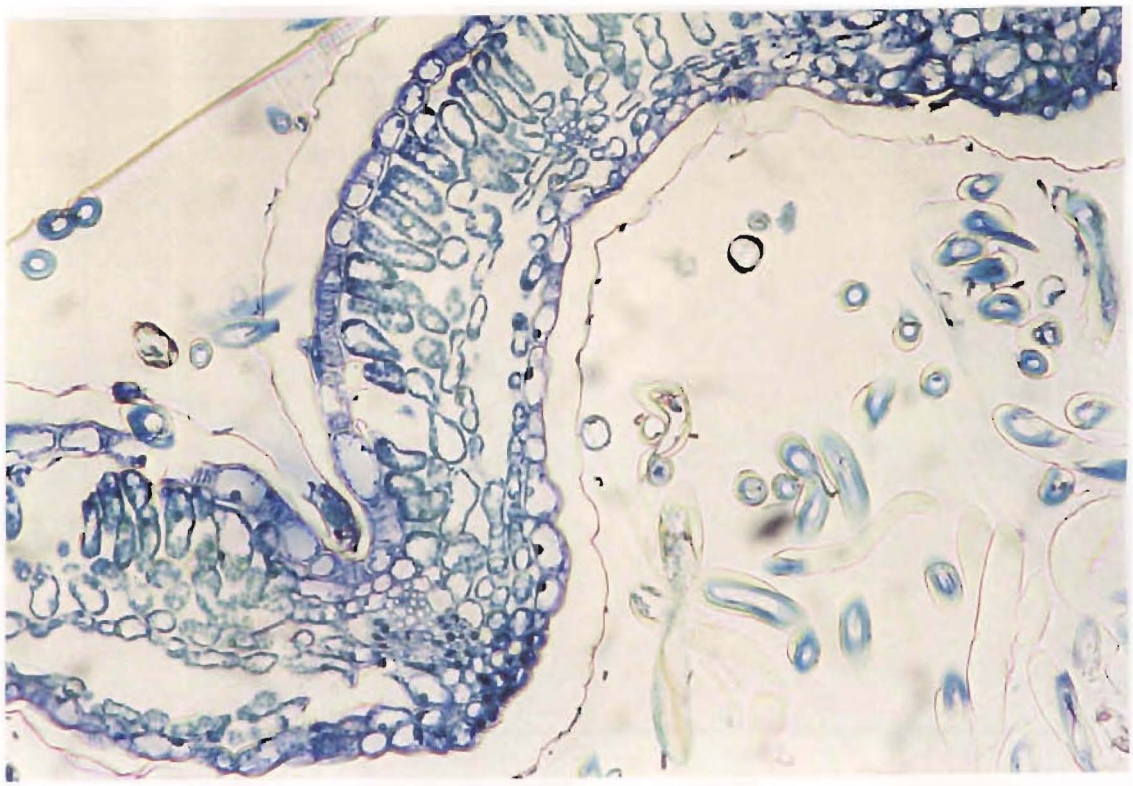


Figure 4.11: Anatomical leaf section of *Haastia recurva*.

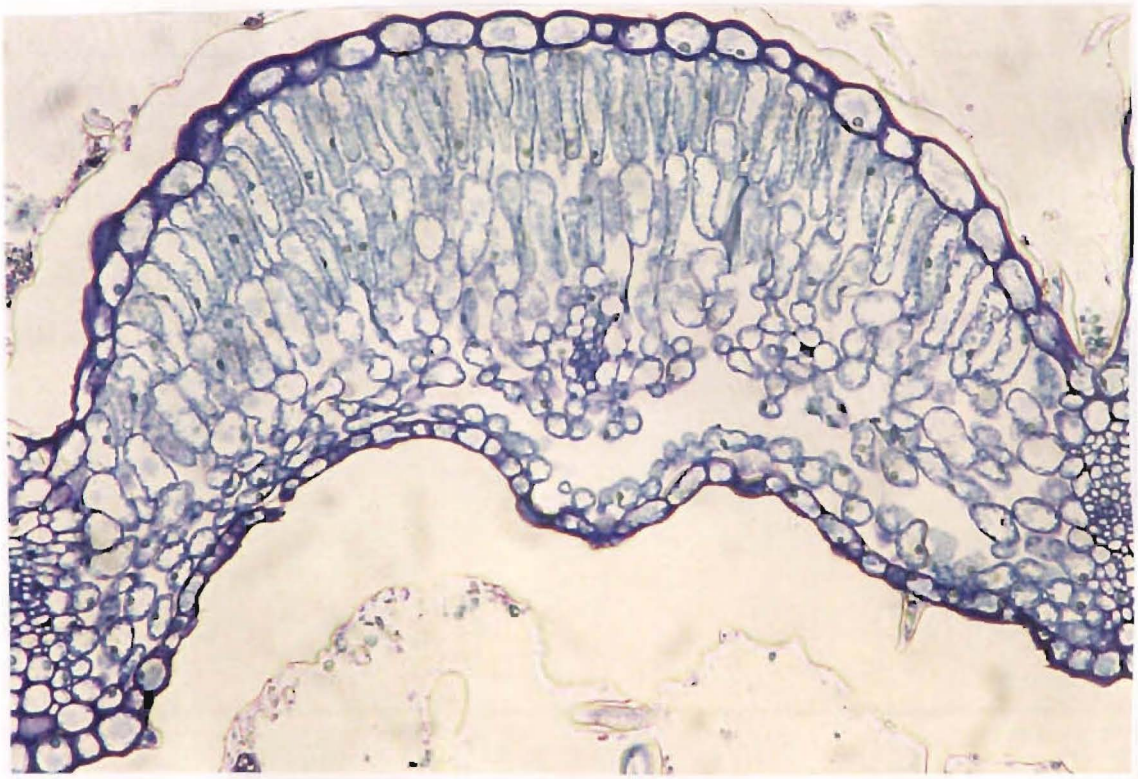


Figure 4.12: Anatomical leaf section of *Haastia sinclairii*.

Figure 4.13: Anatomical leaf section of *Haastia sinclairii* 'Potts'.

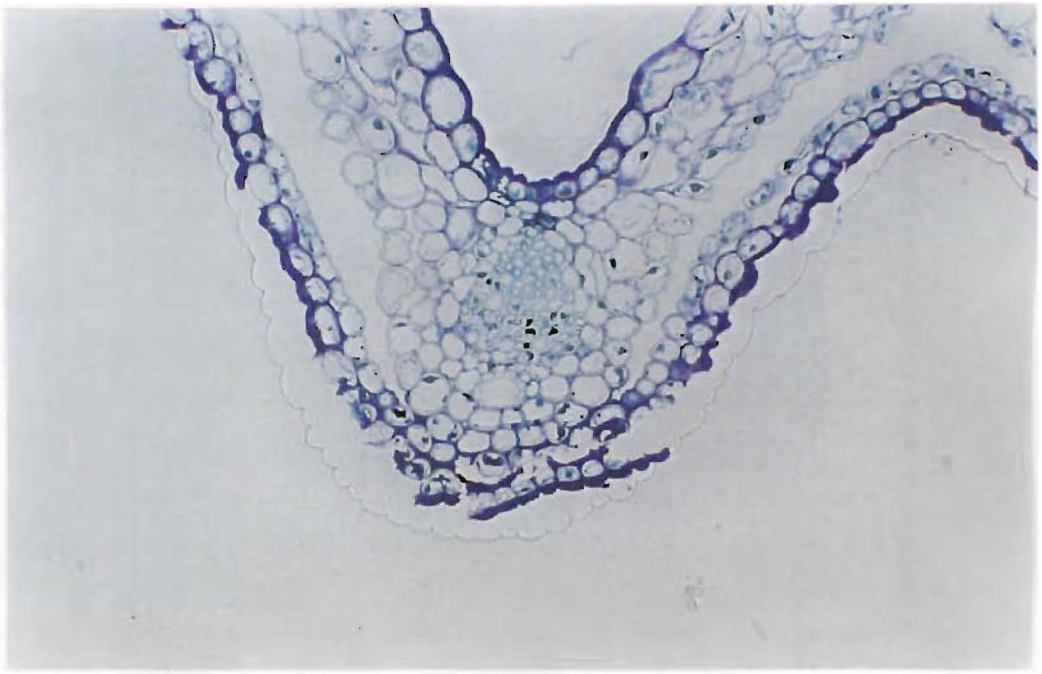


Figure 4.14: Detail of the leaf section of *Haastia pulvinaris* var. *minor*.

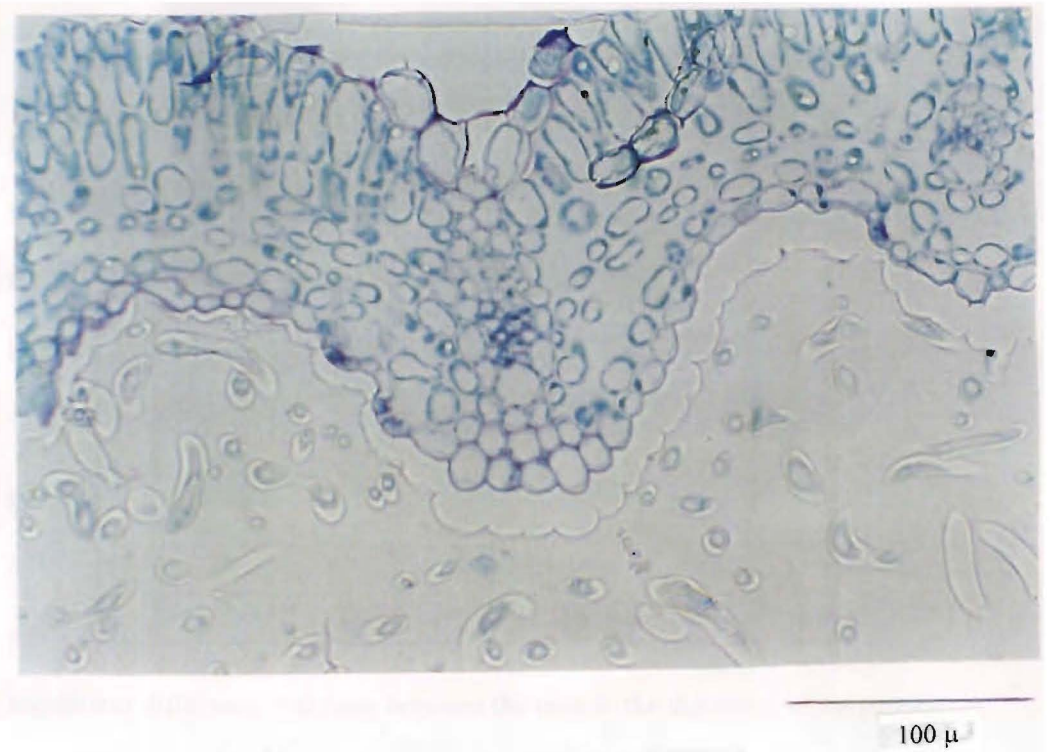


Figure 4.15: Detail of the leaf section of *Haastia sinclairii* 'Potts'.

4.2.2 Other features of note

Bract numbers of each capitulum appear to be a function of the receptacle diameter, and their own length and shape, which is usually approximately uniform. In general, *H. pulvinaris* var. *pulvinaris* has between 20 and 30 bracts on the capitulum, while var. *minor* never has more than 25. *H. recurva* recorded similar numbers to those of *H. pulvinaris* var. *pulvinaris*. *H. sinclairii* has the greatest bract numbers, but also the most variable, usually falling within the range of 24 to 40 per capitulum.

A number of other characters relating to the inflorescence are common. All taxa have greater numbers of hermaphrodite florets within the capitula than they do of female florets. The florets are numerous, and exact numbers of each floret type vary between capitula with receptacle diameter. The female florets are pistillate, and lack the large ligulate corolla commonly found elsewhere in the Compositae (Bentham

1873). In fact, the corolla of this floret type is reduced to a mere sheath or collar at the base of the style. The disc florets are perfect in their parts, with five semi-sagittate anthers clustered around a bifurcate stigma, all protected by a campanulate corolla. The stigmatic surface of both floret types consists of two parallel bars running the length of the inner surface of the stigmatic arm, joining to form a 'horseshoe' at the terminal end. While the style of the hermaphrodite floret may be papillose, that of the pistillate floret is always glabrous. The achenes are long and cylindrical in form, somewhat oblong, and completely glabrous. The single ring of pappus hairs on each floret are long and slender, although somewhat rigid. No significant difference was seen between the taxa in the thickness of the pappus.

Insect predation of the capitula was noted in all taxa. *H. recurva* appears to be particularly susceptible, as insect larva were found to have at least partially damaged over three quarters of all capitula of that species (including var. *wallii*) examined. As noted in chapter 2, this is at least three times the amount of predation seen in any other taxon in the genus.

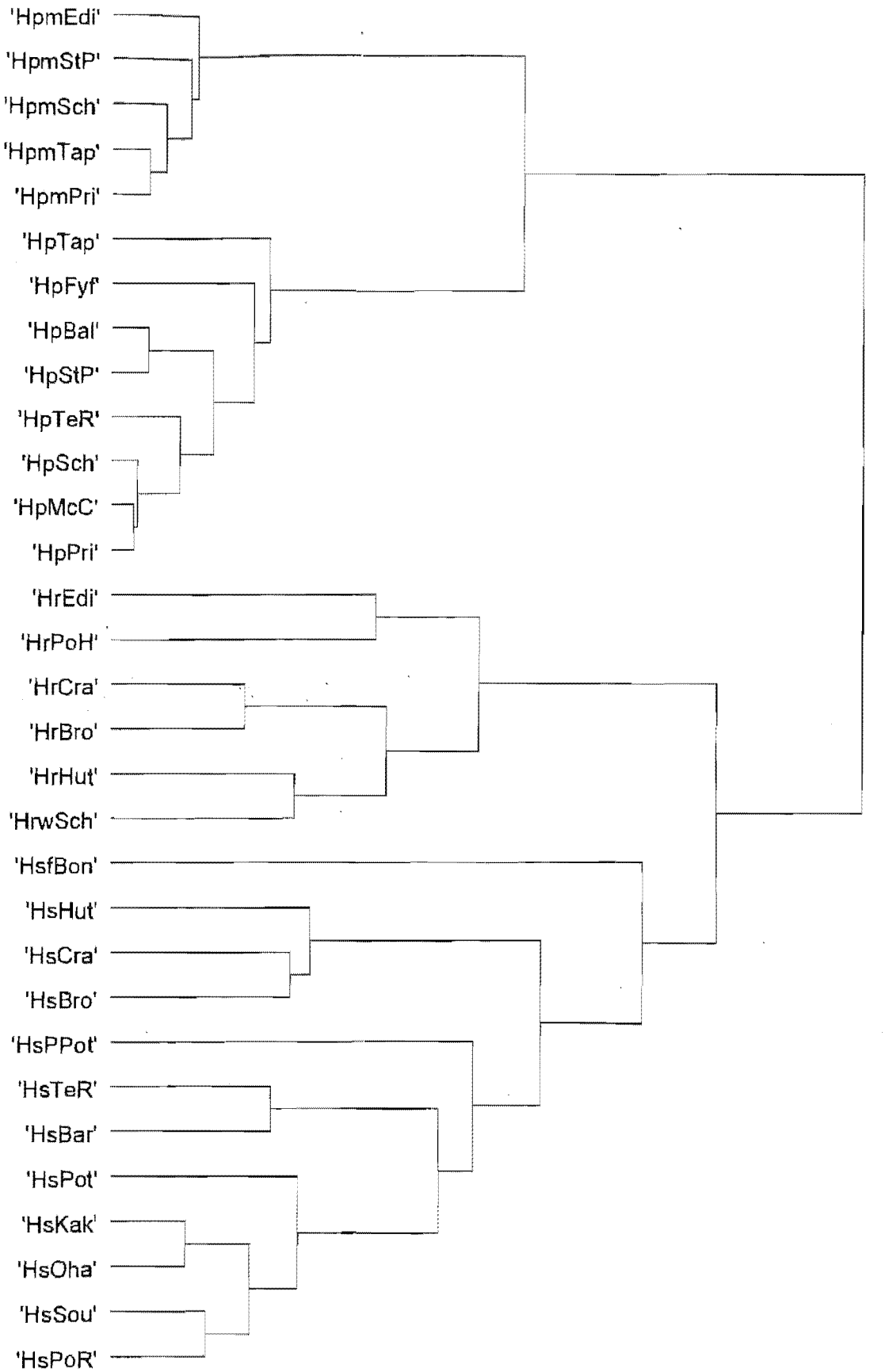


Figure 4. 16: Dendrogram showing the clustering of *Haastia* taxa according to the degree of overall similarity between any two OTUs.

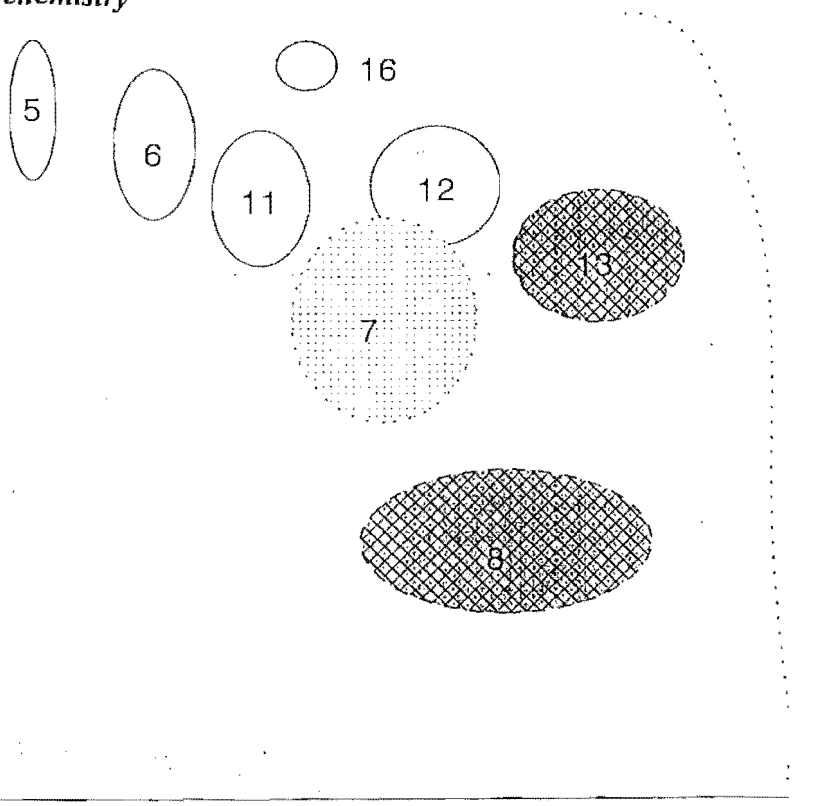


Figure 4.17: Chromatogram of compounds present in the leaves of *Haastia pulvinaris* var. *pulvinaris*.

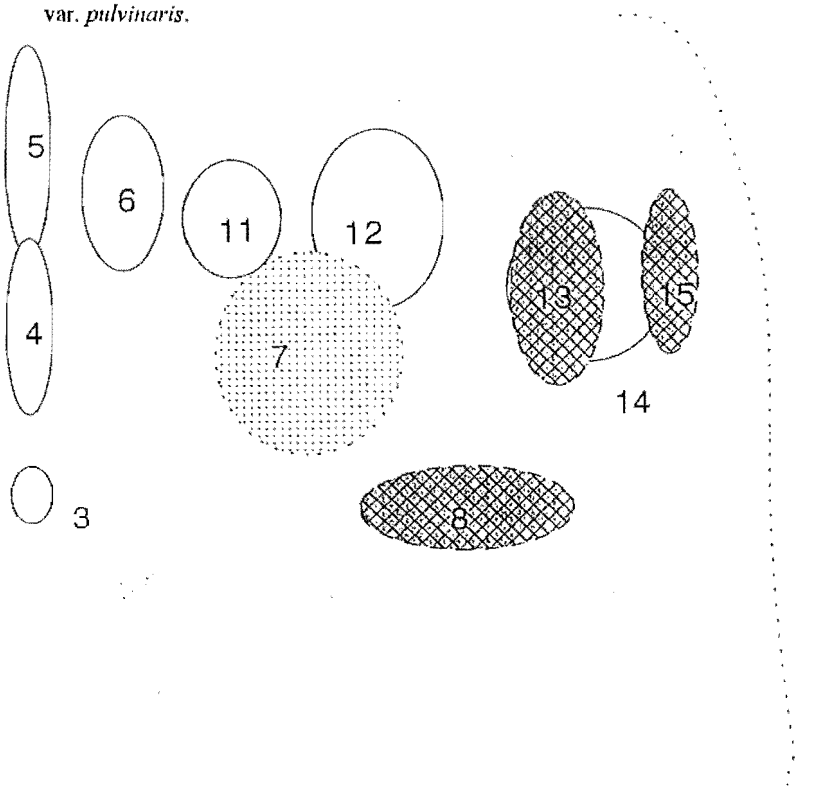


Figure 4.18: Chromatogram of compounds present in the leaves of *Haastia pulvinaris* var. *minor*

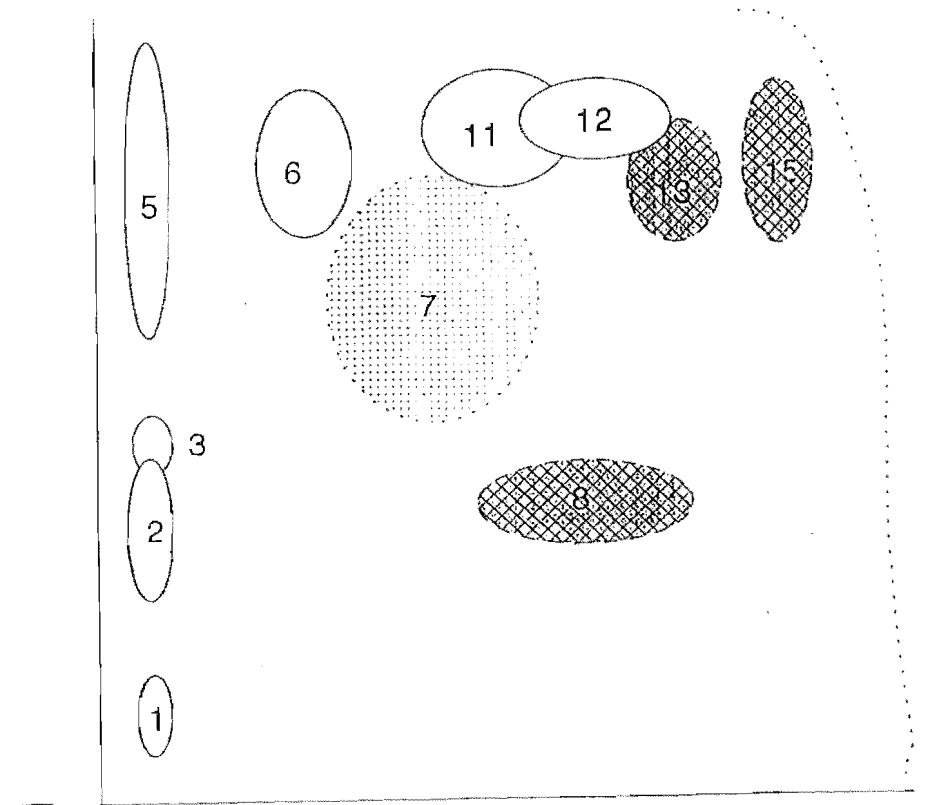


Figure 4.19: Chromatogram of compounds present in the leaves of *Haastia recurva*

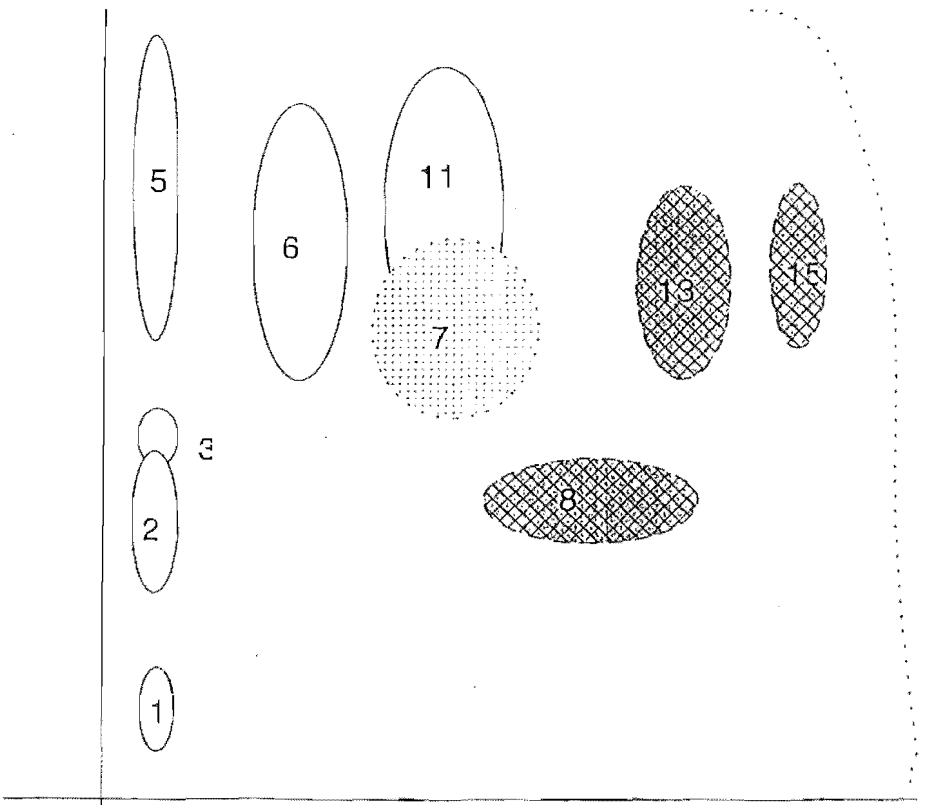


Figure 4.20: Chromatogram of compounds present in the leaves of *Haastia sinclairii*

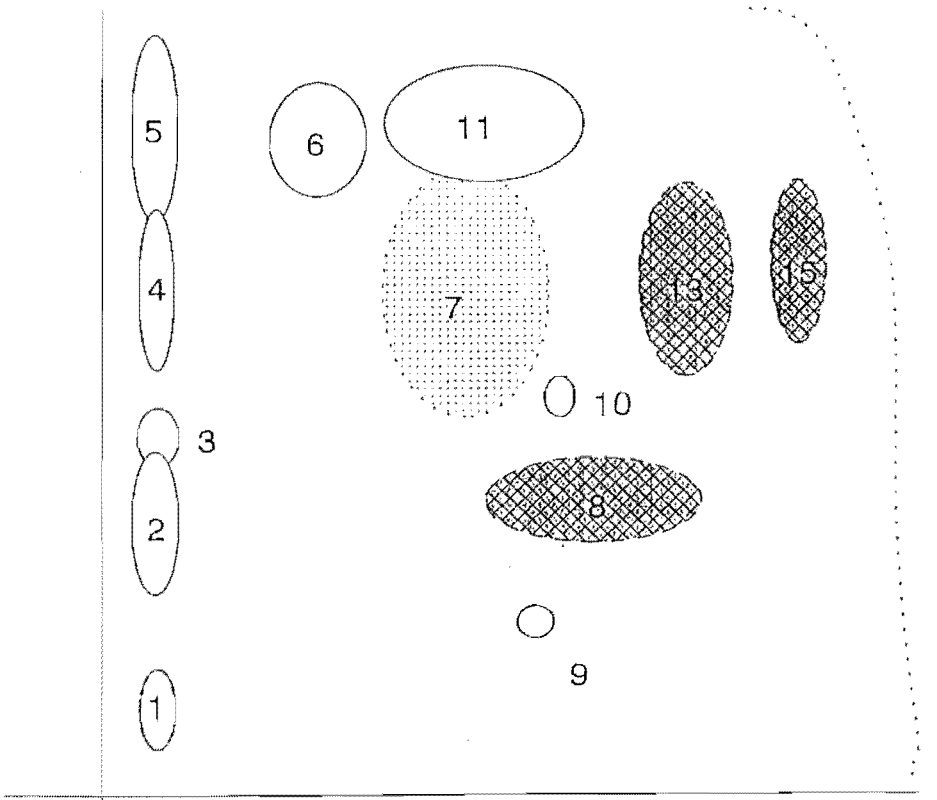


Figure 4.21: Chromatogram of compounds present in the leaves of *Haastia sinclairii* 'Potts'

4.4 Phenology

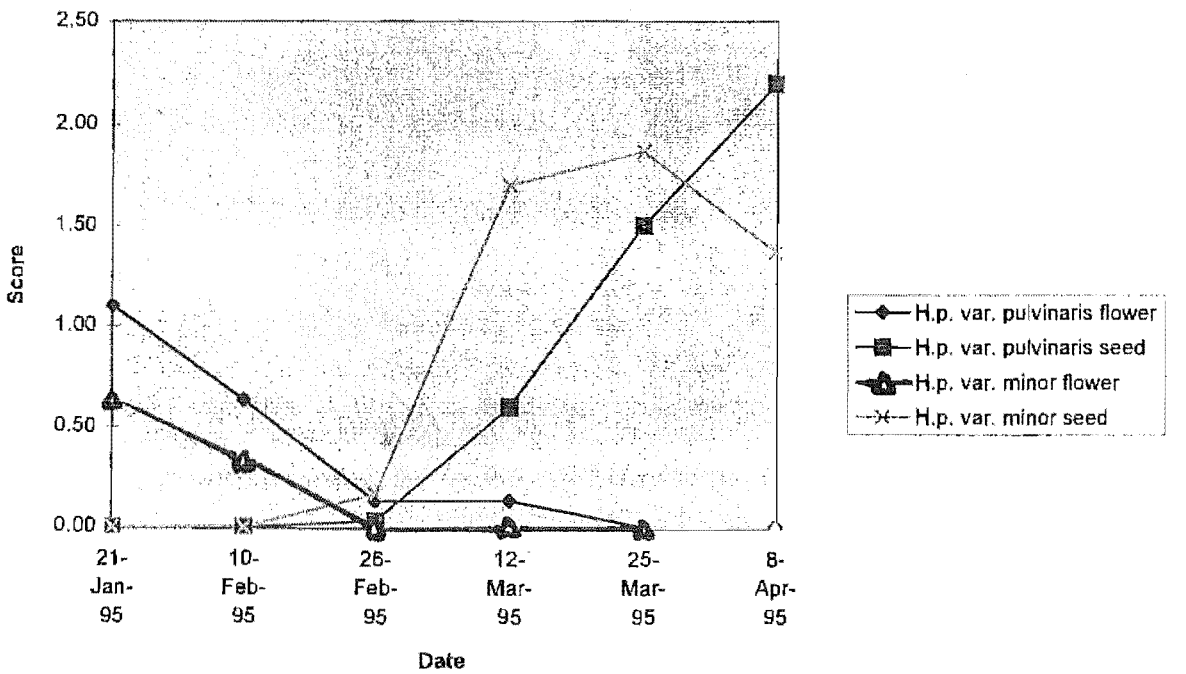


Figure 4.22: Graph of the flowering patterns periods displayed by adjacent populations of *Haastia pulvinaris* var. *pulvinaris* and *Haastia pulvinaris* var. *minor*.

5 Discussion of Results and Conclusions

5.1 Morphology and Anatomy

5.1.1 The Genus

There are several obvious features that all taxa in the group share to some extent. Perhaps most importantly, all the taxa of the genus are restricted to the alpine zone. This is more unusual, in New Zealand at any rate, than one would think. The majority of the genera represented above the snow-line also contain species commonly found in habitats of lower altitude (for example, *Raoulia*, the genus that includes *R. eximia*, the 'other' vegetable sheep, *Ranunculus*, *Gentiana*, and *Leptinella*) (Mark & Adams 1973). Such restriction suggests that the genus is of strictly alpine origin, possibly having radiated from a single alpine ancestor, rather than having originated at lower altitudes and undergoing dispersal to the mountains.

All taxa have a low, sprawling or pulvinate growth form (Table 4.1(a)). None are particularly woody, although there is usually some degree of secondary thickening of the stem (Table 4.1(c)). The general structure of the leaf is similar throughout the genus, consisting of a fleshy lamina mounted on a broad sheathing base. Both faces of the lamina and the abaxial (lower) surface of the sheath are covered in a dense layer of hair. The adaxial surface of the sheath either has a sparser tomentum, or is glabrous. In all the species, the lamina is rubbery to the touch, and inlaid with wrinkles, corresponding to the patterns of venation.

5.1.2 The Species

The three species described by Hooker (1864) may be distinguished from one another by several key features. The most obvious is that of growth form (Table 4.1(a)). *Haastia pulvinaris* has the distinctive pulvinate (cushion-like) form that lends it the nick-name of 'vegetable sheep'. A single cushion may reach over a metre in diameter; larger cushions yet are formed by the aggregation of two or more plants. The cushions are formed by the compacting of the branchlet tips together (Table 4.1(a)), much as described by Hooker (1864). It may be deduced that no light penetrates into the interior of the plant, as all the viable foliage is found at, or just behind, the branchlet apex. Consequently, the leaves on each branchlet are tightly appressed to one another (Table 4.1(a)), so that optimal foliage is presented, probably in order to maximise photosynthesis. Closer investigation shows that only the apex of the lamina on each leaf is exposed, and that the internodes are negligible in length (Table 4.1 (b)).

H. recurva is of a much more open habit (Table 4.1(a)), although still tending to form dense clumps, usually somewhat smaller than the cushions of *H. pulvinaris* (an exception to this was noted on the Craigieburn ski field, where the plants showed a tendency to sprawl). The leaves of this species are small, seldom more than 15mm in total length (Table 4.1(d)), and the lamina is often recurved more than 45° from the plane of the sheath (Table 4.1(d)). The foliage is not nearly so compressed together as that of *H. pulvinaris*, and a comparatively larger part of the lamina is exposed, although the leaf internodes are still rather short, often no more than one millimetre in length (Table 4.1(b)). The leaves of *H. sinclairii* are relatively larger, often reaching a total length of over 20mm (Table 4.1(d)), and the lamina is

generally more erect than is seen on *H. recurva*, or, at least, does not recurve to the same extent (Table 4.1(d)). *H. sinclairii* possesses the most open habit of the three species (Table 4.1(a)), and the leaves have rather longer internodes, usually over two millimetres (Table 4.1(b)). Viable foliage may be found along most of the length of each stem. The growth form itself is variable (Table 4.1(a)). In some cases, the plant has a sprawling habit, with stems cascading over the substrate. Elsewhere, the plant is rhizomous, appearing as a number of small, erect, solitary shoots above the scree. Only when the rhizome is followed to its source is it possible to tell if all are linked to a single plant. This latter form is prevalent in populations of south eastern Marlborough (Mt. Barefell and Mt. Terako), and also of Mid Canterbury (Mt. Hutt and Mt. Potts) (Table 4.1(a)).

The surface of the lamina also helps distinguish the three species (Table 4.1(f)). That of *H. pulvinaris* is blistered between the lines of venation, to the degree that the entire surface is covered with crenellate projections, particularly along the margin. These crenellations vary in length (Table 4.1(g)), even on a single leaf, thus affecting the depth of the marginal sinuses between. This blistering effect is not quite so exaggerated in *H. recurva* (Fig.4.4(a)), but in this species the surface still bulges between the veins, and may be described as bullate (Table 4.1(f)). The lamina of *H. sinclairii*, however, is usually flat, albeit wrinkled (Table 4.1(f), Fig. 4.4(b)), and may therefore be described as rugose.

Other distinguishing features include the presence (or absence) of canals associated with the veins of the leaf, and the nature of the veins of the involucral bracts. Canals were observed in the leaves of both varieties of *H. pulvinaris* (Table 4.3(d); Figs.

4.9, 4.10, 4.14), but not in those of the other two species (Table 4.3(d); Figs. 4.11, 4.12). However, they were noted in the undescribed taxon from Mt. Potts (Table 4.3(d); Fig. 4.13). In *H. pulvinaris* and *H. sinclairii*, the veins of the bracts are simple and unbranched (Table 4.2 (b); Fig. 4.5). This is not the case for *H. recurva* nor for the 'Potts' form, both of which have branched veins (Table 4.2(b); Fig 4.5).

5.1.3 Haastia pulvinaris

Superficially, *H. pulvinaris* var. *pulvinaris* and *H. pulvinaris* var. *minor* are rather similar. Their respective geographical ranges and ecological distributions are very nearly identical, both being found only on the rocky slopes of the mountains of Marlborough, eastern Nelson and North Canterbury. Both possess a pulvinate (cushion-like) growth form, in which the branchlets, of more or less even length, are tightly compacted to form an unbroken surface (Table 4.1(a)). On both varieties, the lamina is extremely convoluted (Table 4.1(f)), forming a crenellate surface that is hidden beneath the dense insulating layer of hairs that cover the leaf.

Upon closer examination, a number of differences become apparent. The most obvious of these is the hue of the foliage. Specimens of *H. pulvinaris* var. *pulvinaris* have a yellow-green colouration (Fig 1.1), while those of *H. pulvinaris* var. *minor* range from a rather dingy buff shade through to a rich gold (Front.; Fig. 1.3; Table 4.1 (c)). This difference in leaf colour may be augmented by the length, density, and colour of the leaf hairs. The shape of the plant also differs. *H. pulvinaris* var. *pulvinaris* has cushions that often exceed a metre in diameter. Those of *H. pulvinaris* var. *minor* are seldom so large, although they are usually comparatively taller (Table 4.1 (b)). In addition, the surface of *H. pulvinaris* var. *minor* cushions is

often quite uneven, almost lumpy, in appearance (Fig 1.3). This is particularly apparent amongst the populations of Marlborough and North Canterbury, although not so in the Nelson populations (pers. obs.).

A point that may cause confusion when making a casual field identification deals with the diameter of the individual branchlets. Those of *H. pulvinaris* var. *minor* are generally of a greater diameter than those of *H. pulvinaris* var. *pulvinaris*, often by several millimetres (Figs. 4.2, 4.3). In light of this, the name given to the variety by Laing (1912) may seem somewhat misleading until examination of the leaf dimensions reveals that it is the individual leaves of *H. pulvinaris* var. *minor*, not the branchlets, that are smaller in total area than those of the type variety (Table 4.1(d), Fig. 4.4(a)).

Leaf shape differs. Specimens of *H. pulvinaris* var. *pulvinaris* were seen to have broad, flabellate leaves (Fig. 4.4(a)), spreading to a much greater width than that of the sheaths (Table 4.1(e)). The leaf apex forms a smooth arc (Table 4.1(f)). The lamina shape of *H. pulvinaris* var. *minor* tends to be rather narrower (Fig. 4.4(a)), spreading little from the base (Table 4.1(e)), with an apex that is often rather more truncate (Table 4.1(f)). In addition, the sheath length in the specimens of *H. pulvinaris* var. *minor* that were examined was usually significantly longer than was seen in *H. pulvinaris* var. *pulvinaris* (Table 4.1(d)).

Discrepancies between the two forms were also noted when the floral morphology and structure of the inflorescence were studied. Firstly, the shape of the involucral bracts is different (Fig. 4.5). In the type variety, the bracts, being widest at the top,

are obovate, while those of *H. pulvinaris* var. *minor* are ovate, being widest at the base (Table 4.2(b)). Additionally, the bracts of *H. pulvinaris* var. *minor* seem to show a tendency to be slightly broader overall (Table 4.2(a)).

The corolla tube of the female florets is of different lengths in the two varieties. In *H. pulvinaris* var. *pulvinaris*, this tube is relatively long, enclosing roughly half the length of the style. The corolla is much shorter on the pistillate florets of *H. pulvinaris* var. *minor*, barely more than a collar at the base.

The structure of the stigma on the hermaphroditic florets is a useful character. While both varieties have papillose stigmatic apices, only on *H. pulvinaris* var. *minor* are the papillii short, and evenly distributed over the surface (Table 4.2(c)). The ends of the stigmatic arms of *H. pulvinaris* var. *pulvinaris* are surmounted by three tufts of longer hairs, two lateral and one at the apex.

The leaf anatomy is similar in most respects other than two features. The first of these deals with the comparative depth (longitudinal dimension) of the abaxial and adaxial epidermal cells. The specimens of *H. pulvinaris* var. *pulvinaris* have epidermal cells on the abaxial surface that are more shallow than, or equal to, those on the adaxial surface (Table 4.3(a); Fig. 4.9). The abaxial epidermal cells of *H. pulvinaris* var. *minor* are generally deeper than the adaxial cells (Table 4.3(a); Fig. 4.10). The second feature deals with the arrangement of the palisade cells. In the leaf sections of *H. pulvinaris* var. *minor*, the palisade cells are closely packed and are of uniform length, while those of *H. pulvinaris* var. *pulvinaris* are uneven in both length and arrangement (Table 4.3(c); Figs. 4.9, 4.10).

A short interval between the peak flowering times of the two forms was apparent in the data collected from the site on Mt. St. Patrick (Fig. 4.22), possibly due to the disparity in environmental conditions on either side of the summit (Rathcke & Lacey 1985). There was certainly no conclusive evidence of temporal separation that may have isolated the two forms from one another, as the flowering periods overlapped for an extended length of time (Fig. 4.22). Populations of the two forms in similar situations elsewhere were observed to be flowering simultaneously (pers. obs.).

5.1.4 Haastia recurva

Leaf colour and geographical distribution are the major features that may be used initially to distinguish the two varieties of *Haastia recurva.* The type form, *H. recurva* var. *recurva,* occurs locally throughout North Canterbury and south-east Nelson (the type locality is Tarndale (Allan 1961)), and possibly Marlborough (see below). The leaves are usually silver (Table 4.1(c)), although a colour polymorphism was observed on two of the North Canterbury sites, Poulter Hill and Broken River (Table 4.1(c); Fig. 1.4). In these cases, it was estimated that approximately three fifths of the plants in the population are silver or grey in colour, while the remainder are bronze (pers. obs.). *H. recurva* var. *wallii* occurs further north, around the headwaters of the Waihopai, Acheron and Awatere Rivers, in Marlborough, and is yellow-green in colour (Table 4.1(c); Fig. 1.5).

Although *H. recurva* var. *wallii* is reported to be present in both the Seaward Kaikoura and Inland Kaikoura Ranges, no personal collections of this taxon were made from either of these regions, nor was there any confirmation in the literature.

Identification of herbarium specimens from these mountains is uncertain, as no floral parts are evident on the few specimens available, and vegetative characters are not definitive. It is possible that these are in fact samples of *H. recurva* var. *recurva.*

Contrary to the descriptions of both Cockayne (1918) and Allan (1961), the leaves of *H. recurva* var. *wallii* do not appear to be significantly smaller than those of *H. recurva* var. *recurva* (Table 4.1(d)), although a higher degree of recurvature (Table 4.1(d)) and a rather pointed leaf apex (Table 4.1(f)) may make them appear so. The capitula of *H. recurva* var. *wallii* are narrower, reaching diameters no greater than two thirds that of the larger capitula of *H. recurva* var. *recurva* (Table 4.2 (a)). There appears to be little difference in the length of the involucral bracts between the two forms (Table 4.2(a)).

Although blistering of the lamina is moderate in the majority of the populations of the species (including *H. recurva* var. *wallii*) (Table 4.1(f)), more exaggerated blistering was observed from samples of the Mt. Edison population, to the extent that the crenellations of *H. pulvinaris* are beginning to appear. This may be due to the effects of introgressive hybridisation (*sensu* Davis & Heywood 1963). A large population of *H. pulvinaris* var. *minor* is also present at this site, and several obvious *H. recurva* x *H. pulvinaris* var. *minor* hybrids were observed (Fig 5.1). It is entirely possible that the effects of crossing between the two species is wider than has been previously believed, at least in this situation.

The florets of *H. recurva* var. *wallii* appear to be longer, relative to the length of the involucral bracts, than those of *H. recurva* var. *recurva* (Table 4.2(c)). However,

this may not be particularly significant, as the population of *H. recurva* var. *wallii* at Mt. Schiza was sampled at a later time during the flowering period than the *H. recurva* var. *recurva* populations, and so had more time in which to develop and elongate. The shorter length of the pappus hairs, relative to the floret length, is consistent with this explanation (Table 4.2(c)). It does suggest, though, that the florets of the two forms are actually of similar lengths when fully developed.

The only feature of leaf anatomy that separates the two forms is in the arrangement of the palisade cells. Those of the type variety are organised in an orderly fashion, in a single, closely packed rank, and the cells themselves are of relatively even lengths (Table 4.3(c)). The palisade cells of *H. recurva* var. *wallii* could be described as somewhat chaotic in their arrangement, with large spaces apparent between the cells, and a distribution that is not uniform over the surface of the lamina (Table 4.3(c)). No canals were seen in the lamina sections (Table 4.3(d)).

5.1.5 Haastia sinclairii

Haastia sinclairii has the largest range of the three species, and is the most variable in its features. However, the leaf shape is always obovate or oblong, with the lamina being most commonly widest at its base, with an obtuse apex (Table 4.1(f); Fig. 4.4(b)). The sheath is narrower or the same width as the lamina (Table 4.1(e)), the fan shape of *H. pulvinaris* is not seen. The lamina itself has a relatively flat surface (Table 4.1(f)), although some blistering is apparent in the Broken River and Craigieburn populations.

It may be seen that the angle of leaf recurvature is generally less in the leaves of *H. sinclairii* than it is in the other species (Table 4.1(d)). This is particularly true of the Marlborough and Nelson populations, which appear to have rather erect leaves with little recurvature, no more than 30° from the axis of the sheath. All other populations of this species, including those of *H. sinclairii* var. *fulvida* and the 'Potts' form, have leaves that recurve between 40° and 60°.

Along with the variety described by Allan (1961), and the unusual population from Mt. Potts that was temporarily grouped with the species, one other distinct form may be distinguished in the populations of Nelson, Marlborough and Canterbury.

The habit of this form is rhizomatous (Table 4.1(a)), appearing as a few erect shoots in the scree (occasionally two or three may be clustered together (Fig. 4.6)), up to 100 mm in height (Table 4.1(b)). The pale grey leaves (Table 4.1(c)) are large, often over two centimetres long (Table 4.1(d)) and over a centimetre wide, and held rigidly erect, as noted above. The angle of recurvature of the lamina exhibited in these populations was the smallest seen throughout the genus (Table 4.1(d)). The lamina is obovate, with a rounded apex (Table 4.1(f); Fig. 4.4(b)). The capitula are also large, up to 15 mm in diameter at the receptacle (Table 4.2(a)), but spreading to twice that width at the rim of the bracts (Fig. 4.7). This was seen at only two sites, Mt. Terako and Mt. Barefell, although examination of herbarium sheets reveal that similar populations may also be found on the Inland and Seaward Kaikoura Ranges.

The length of the bracts themselves, and of the florets, is the greatest seen in the genus. The bracts are linear (Table 4.2(b), Fig. 4.5)), only one millimetre wide, but

up to two centimetres long (Table 4.2 (a)). The apex is apiculate (Table 4.2(b)) Two veins may be traced in each bract (Table 4.2(a)). The florets are of comparable lengths with the bracts, often reaching 15 mm or greater (Table 4.2(c)). The corolla tube of the female floret is approximately two fifths the total length of the style (Table 4.2(c)).

The remainder of the *H. sinclairii*, excluding *H. sinclairii* var. *fulvida* and the 'Potts' form, is somewhat variable in habit and leaf size. In North Canterbury a decumbent habit was usually observed (Table 4.1(a)), similar to that of the type (collected from the Wairau Pass (Allan 1961)), although the population on the Poulter Range rather tended to sprawl. A sprawling habit was also noted from the Kakapo Peak population, in North West Nelson, and also from the Ohau ski-field, in South Canterbury (Table 4.1(a)). At the other sites, Mt. Southey, in eastern Nelson (incidentally, quite close to the type locality), Mt. Hutt and Mt. Potts in Mid Canterbury, a rhizomatous habit was seen, similar to that of the Mt. Te Rako and Mt. Barefell populations (Table 4.1(a)).

It could be argued that the difference between the decumbent and rhizomatous forms is merely a function of the environment, particularly of the substrate. On shallow screes or broken ground, the entirety of the plant is above the surface (Fig. 1.6). On deeper, mobile screes, the plant is buried, so that only the tips of the branches appear above the surface (pers. obs.). However, this theory does not appear to apply to the Marlborough and Amuri populations, where the habit is consistently rhizomatous, even though specimens were found growing on a range of scree types.

The lamina of the leaves is usually slightly shorter than broad (Table 4.1 (e); Fig. 4.4(a)), although it is not unusual to find longer, narrow leaves in any particular population. Leaf shape and size is possibly the most variable of the characters measured. However, a trend was noticed that the average leaf length gets longer with latitude, i.e. long leaves are more common in the southern populations (Table 4.1(d)). The colour of the lamina varies between silver and a rather dark grey (Table 4.1 (c); Fig. 1.6), although this may be partially attributed to the amount of dirt caught between the leaf hairs. The leaf apex is obtuse (Table 4.1(f)).

The lamina surface of specimens from three of the Canterbury populations; Craigieburn, Broken River and Mt. Hutt, were rather more blistered than was observed elsewhere (Table 4.1(f)). This may be the result of some degree of hybridisation with adjacent *H. recurva* populations, in a similar situation to that already noted on Mt. Edison.

The capitula vary in size between 5 and 12 mm in diameter at the receptacle, seldom spreading any wider at the top (Table 4.2(a)). The bracts are linear in shape (Table 4.2(b); Fig. 4.5), and rather narrow, often under a millimetre in width, although they reach lengths of over a centimetre (Table 4.2(a)). There is only a single vein in each bract (Table 4.2(a); Fig. 4.5).

The florets range in length between 5 and 9 mm, around two thirds the length of the bracts (Table 4.2(c)), although exact length at the time of measurement was dependant upon the stage of development. In all cases, the corolla tube was reduced

to a collar at the base of the style, around a tenth of the total length of the floret (Table 4.2(c)).

Anatomical characters appear to remain consistent throughout both these forms of *Haastia sinclairii*, or vary randomly, following no consistent trends. The epidermal cells on the abaxial surface may be smaller, larger, or be of equal dimensions with those on the adaxial surface (although equal dimensions were most often seen) (Table 4.3(a); Fig. 4.12). The mesophyll cells exhibit non-uniform size, shape and distribution, even in the same leaf (Table 4.3(d)). The palisade cells are closely packed and of uneven lengths, although those seen in specimens of the Marlborough populations appeared to be consistently larger and thicker than palisade cells from elsewhere (Table4.3(c)). There were no signs of canals of any form in any of these specimens (Table 4.3(d); Fig. 4.12).

The single variety of *H. sinclairii* described by Allan (1961) is restricted in distribution to the mountains of Fiordland and western Otago. *H. sinclairii* var. *fulvida* may be distinguished in the field from the rest of the species by the leaf colour and the shape of the lamina. The lamina is much greener than was seen in the populations further north (Table 4.1(c)), due to the sparsity of the leaf hairs, allowing a greater portion of the lamina surface to be visible. The leaves are consistently long and narrow (Table 4.1(e), Fig. 4.4(b)), with a rounded apex (Table 4.1(f)). The angle of leaf recurvature exhibited by this form is the highest seen in the species, over 60° (Table 4.1(d)) (although this still falls short of the angle of recurvature commonly seen in *H. recurva* and *H. pulvinaris*).

H. sinclairii var. *fulvida* has a sprawling growth form (Table 4.1(a)), and appears to prefer growing on clay based fell-field or in rock crevices (Fig. 1.8), over deeper screes. However, specimens were found growing in both habitats.

The capitula are approximately the same diameter as those of the Canterbury populations (Table 4.2(a)), but the involucral bracts (Table 4.2(b); Fig. 4.5) are slightly shorter and significantly broader (Table 4.2(a)). There are two simple veins in each bract (Table 4.2(a); Fig. 4.5). A feature of the capitulum not seen elsewhere in the genus is the appearance of a 'collar', formed by a thick section in the lower part of each bract (Fig. 4.5).

There are no significant differences in floret morphology between *H. sinclairii* var. *fulvida* and the other populations of *H. sinclairii*, save that the corolla tube of the female floret is relatively long, two fifths the total length of the style (Table 4.2(c)).

An unusual anatomical feature seen in leaf sections of *H. sinclairii* var. *fulvida* is the uniformity of the cells. All the epidermal cells observed on each section were approximately the same size and shape (Table 4.3(a)), as were the palisade and mesophyll cells (Table 4.3(d)). Such uniformity in all cell types is not apparent elsewhere in the genus. Another notable feature concerns the distribution of the palisade cells. These were not seen in sections taken from the middle or lower part of the lamina, but only from the apex, where they were much shorter than the average palisade cell length of the rest of the species.

The undetermined taxon found on Mt. Potts is similar to *H. sinclairii* var. *fulvida* in several features. The habit is similar, with the plant forming decumbent clumps up to a metre in width (Table 4.1(a); Fig. 1.7). The leaf shape is similar to that of *H. sinclairii* var. *fulvida*; longer than it is broad (Table 4.1(e)), with a rounded apex (Table 4.1(f); Fig. 4.4(b)). The lamina is a olive green colour (Table 4.1(c); Fig 1.7), although not as bright as that of *H. sinclairii* var. *fulvida*. However, a feature that is not seen in *H. sinclairii* var. *fulvida*, or anywhere else in the genus, is the elongation of the internodes on branchlets bearing the capitula (Fig. 4.8), so that these are borne above the foliage rather than amongst it (Table 4.2(a)).

The capitulum is of approximately the same diameter as that of *H. sinclairii* (Table 4.2(a)), but the bracts are shorter (Table 4.2(a)), and elliptic in shape (Table 4.2(b);Fig. 4.5), widening in the mid-section. There is only a single vein in each bract (Table 4.2(a); Fig. 4.5), but this branches three or four times (Table 4.2(b)), in a similar fashion to that of *H. recurva* var. *recurva*. The florets and pappus hairs are shorter than those of *H. sinclairii* (Table 4.2(c)), even when sampled at the peak of the flowering season. The corolla sheath on the female florets is relatively long, over one third the length of the style (Table 4.2(c)). The pappus hairs are not united at the base (Table 4.2(c)).

The basic anatomy of the leaf is similar to that of *H. sinclairii* and other taxa in the genus. There is little uniformity of cell size (Table 4.3(a)), although there is no consistent difference between the epidermal cells of either surface. The palisade cells are loosely arranged (Table 4.3(c); Figs. 4.13, 4.15). A feature that is seen here

and in the two forms of *H. pulvinaris*, but not elsewhere in *H. sinclairii* or *H. recurva*, is the presence of canals associated with the veins (Table 4.3(d)).

5.2 Results of the Numerical Phenetic Analysis

There are two parts to the dendrogram produced by the numerical phenetic analysis of the genus (Fig. 4.16). The first of these contains two tight clusters that represent the pulvinate taxa. They are shown to be quite distinct from one another, with relatively little difference between the populations. In fact, the *H. pulvinaris* var. *minor* cluster indicates that all of the populations of this taxon are covered by a similarity factor of 95%. Interestingly, what variation there is in the taxon has sorted out geographically, with the Nelson and Marlborough populations being most closely linked to one another. Slightly more variation is evident in the cluster representing the type variety of *H. pulvinaris*, although all populations still fall within the 90% similarity mark. However, here the variation does not appear to be linked to geography. The populations of Mt. Princess, Mt. McCabe (both Nelson) and Mt. Schiza (Marlborough) cluster tightly together, with the Mt. Terako population (North Canterbury) linking to this group. The Balaklava (Nelson) and Mt. St. Patrick (North Canterbury) populations form another sub-cluster. The two populations from eastern Marlborough, those of Tapu-ea-nuku and Mt. Fyffe, appear as relative outliers to the main group.

On the other part of the dendrogram, there is considerably more variation within the clusters. The main part of the *H. recurva* cluster consists of four populations, all within an approximate similarity factor of 85%. The two Craigieburn populations, Craigieburn Valley and Broken River, form one cluster, but the other mid-

Canterbury population, that of Mt. Hutt, appears to be more closely linked to the population of *H. recurva* var. *wallii* from Mt. Schiza. These latter two populations are also shown to be relatively closely linked. The populations of Mt. Edison and Poulter Hill (North Canterbury) form another loose pairing.

The greatest amount of variation between the populations of a species may be seen in the cluster of *H. sinclairii* and its associated taxa. Within the main cluster, a number of sub-clusters may be distinguished. The populations of Mt. Barefell and Mt. Terako are linked together, a coupling that is significant due to the geographical situation of these two sites. The population of *H. sinclairii* on Mt. Southey, the other site in that general area, where Nelson, Marlborough and North Canterbury intersect, is not closely connected to these two populations. Instead, it appears to have more in common with the Poulter Range population, from close to the Main Divide. This pairing also clusters with the pairing of the Kakapo Peak and Ohau populations. The Mt. Potts population of *H. sinclairii* is a slightly distant part of this cluster.

The other loose sub-cluster in this group is that of the Craigieburn Valley, Broken River and Mt. Hutt populations. All of these three populations are geographically close, but the degree of similarity between the three is not as high as that of other clusters, being less than 90%.

The population of *H. sinclairii* var. *fulvida* forms a distant outlier to the main cluster, as may be expected. The 'Potts' form of *H. sinclairii* links closer to the main group, but does not form a pair or cluster with any others; certainly not with the population of *H. sinclairii* found at the same site.

5.3 Hybridisation

Given that the phenomenon of hybridisation in the genus has remained undocumented, the observed incidence of interspecific hybrids is surprisingly high. The flowering season of all taxa in the genus is strictly limited by the relatively short period of time between the spring thaw and the first snow of autumn. All activity such as flowering, seed dispersal, and growth must take place during this time. Consequently, there is not the length of time available for the staggered flowering periods seen between several species of *Raoulia* (not including *R. eximia* and the other alpine species of *Raoulia)*(A. Wilton, pers. comm.) and other New Zealand composites found at lower altitudes. Although there may be some variation in peak flowering times, due to environmental conditions, anthesis is more or less simultaneous for adjacent populations (Fig. 4.22). Therefore, if pollination vectors are shared, there is little barrier to cross-pollination within a given locality.

The dominant pollinator (if, in fact, such exists) was not identified. Although several species of butterflies and beetles were seen visiting the open capitula, transferral of pollen was never actually observed. However, it is unlikely that any such vectors would transfer pollen over distances greater than one or two kilometres (Kay 1976), making the proximity of the parental populations almost a necessity.

Crosses between pulvinate and non-pulvinate species are particularly conspicuous. Putative F_1 hybrids between *Haastia recurva* and *H. pulvinaris* var. *minor* were seen at Mt. Edison, growing amongst the *H. recurva* population (Fig. 5.1). F_1 hybrids between *H. recurva* var. *wallii* and one of the two varieties of *H. pulvinaris*

(populations of both were in the immediate vicinity) were also noted on Mt. Schiza. Again the hybrids occurred only amongst the *H. recurva* population, suggesting that *H. recurva* is the maternal parent in these cases. Such hybrids combine the cushion habit and crenellate lamina of *H. pulvinaris* with the longer leaf shape of *H. recurva*, giving rise to a plant with very compact foliage, tightly pressed together, but that lacks the smooth exterior of the true pulvinate plants (Fig. 5.1). A consistent feature of these hybrids is the density and length of the tomentum, which gives the leaf a rather 'fluffy' appearance, possibly inherited from the pulvinate parent.

Another hybrid specimen was collected by David Norton from the head-waters of the Maruia River. Upon examination, this was seen to combine the pulvinate habit with the leaf shape of *H. sinclairii*, which is common in the vicinity, along with *H. pulvinaris* var. *minor* (Dr. D. Norton, pers. comm.). Other than this, the specimen exhibited all the characters noted above.

Hybrids of other parental combinations are not evident, if they exist at all. *Haastia sinclairii* and *H. recurva* are similar enough in appearance that any intermediates are likely to be masked within the margin of variation. A similar situation applies to the two pulvinate taxa. A much more rigorous analysis, possibly of a biochemical or molecular nature, of any suspected F_1 hybrids, along with the presumed parents, would be necessary to prove the case for either of these two combinations.

Despite this uncertainty as to the presence of first generation hybrids between parents of similar form, features exist in several populations that may be interpreted as evidence of introgressive hybridisation (*sensu.* Davis & Heywood 1963: 466) For

example, a number of specimens of *H. sinclairii* from three populations, Craigieburn, Broken River, and Mt. Hutt, were observed to have laminas that were significantly more blistered than is usual for that species. In all three of these cases, populations of *H. recurva* grow on adjacent slopes. In a similar manner, many of the plants of *H. recurva* of the Mt. Edison population, other than the putative F_1 hybrids,

Figure 5.1: A putative hybrid of *Haastia pulvinaris* and *Haastia recurva*, Mt. Edison.

have crenellate leaf surfaces, although not quite to the same degree of the plants of *H. pulvinaris* var. *minor* growing nearby. Elsewhere, specimens of var. *minor* from Tapu-ae-nuku and Mt. Princess, sites that are shared with adjacent populations of *H. pulvinaris* var. *pulvinaris*, have branchlets that are of a notably lesser diameter than is normally recorded for that taxon. Although these aberrations of morphology may be explained by natural variation, it appears rather a coincidence that such variation is only seen in populations that co-occur with other taxa of the genus. Possibly, this

is instead the result of successive generations of back-crossing between hybrid plants and the parental population.

Hybridisation between the various taxa of the genus, particularly between the pulvinate and non-pulvinate species, suggests that it is highly likely that the group is monophyletic, sharing a single common ancestor, and not, as Merxmüller *et al.* (1977) suggest, belonging to two separate genera (and possibly two different tribes). Such crossing is usually only possible when the taxa concerned are closely related (Davis & Heywood 1963: 462), and at least partially compatible in terms of fertility.

5.4 Biochemistry

Three different compound types, distinguishable by colour, are apparent on the chromatograms (Figs. 4.17-4.21) . Each compound, if present, is represented by a spot (or possibly spots), located approximately in the same position on each chromatogram.

The large yellow spot, #7, and the slightly smaller yellow/green spot, #8, are present in the same location on the chromatogram of each taxon. The yellow/green spots, #13 and 15, were also consistently present for all taxa, bar *H. pulvinaris* var. *minor*, where only spot #13 was visible (Fig. 4.18). However, this was comparatively larger, and may have simply been an amalgamation of the two spots visible elsewhere.

The smaller blue spots exhibit the greatest amount of variation between the chromatograms. *Haastia sinclairii* and *Haastia recurva* share the most similar patterns, differing only by the presence of a single spot, #12 on the *H. recurva*

chromatogram (Fig. 4.19). The chromatogram of the 'Potts' form is also rather similar (Fig. 4.21), lacking spot #12, but showing two smaller spots in the mid section of the graph, #9 and 10.

The two pulvinate species exhibit rather more variation in their chromatograms. The longitudinal line of four or five spots on the left of the other chromatograms is partly missing for *Haastia pulvinaris* var. *minor* (Fig 4.18), almost entirely so for *H. pulvinaris* var. *pulvinaris* (Fig 4.17). Both species display spot #12, missing in *H. sinclairii* and the 'Potts' form. *Haastia pulvinaris* appears to lack the relatively large spot #14, overlapping spots #13 and 15 in the graph of var. *minor*, but this may be due to the larger size of spot #13 in *H. pulvinaris*, obscuring spot #14. *H. pulvinaris* is the only taxon to exhibit spot #16, near the top of the chromatogram.

It should be noted that , while there are clear trends apparent in these results, there does not seem to be any correlation with the results of a similar investigation, taking in all of the gnaphalioid genera of New Zealand (including *Haastia*) carried out by Breitwieser & Ward (1993). It is not known why this is so.

5.5 Treatment of taxa

In the past, there has been some confusion in the literature as to the identity of the two forms of *Haastia pulvinaris*. The description of *H. pulvinaris* var. *minor* by Laing (1912) is very brief, and somewhat ambiguous, making identification from the description alone uncertain. It could be easily applied to either form. Mark & Adams (1973), in the only illustrated comparison between the two varieties, present the yellow/buff form with thick branchlets as the type variety, and the greener form

with slender branchlets as *H. pulvinaris* var. *minor*. However, examination of the type specimen of *H. pulvinaris* var. *minor* that Laing originally described, now at the Landcare Herbarium at Lincoln, reveals that the leaf shape is long and narrow, a characteristic of the yellow form. Given this evidence, it is to this form that the name is applied in this thesis. The type specimen of *H. pulvinaris* is kept at the Herbarium of the Royal Botanical Gardens at Kew, and is therefore not immediately available for direct inspection, although quality photographs were obtained. This makes it rather difficult to determine the nature of the form originally collected by Sinclair and sent to Hooker for description. It is even possible that the same form has been inadvertently described twice! However, until such a time as the type specimen may be examined directly, it must be assumed that the type variety of *H. pulvinaris* is the greener form with slender branchlets and short, flared leaves.

When all of the factors described in the previous sections are taken into account, there is no doubt that these two taxa are not varieties of the same species, but rather two separate species, albeit more similar to one another than they are to any of the other taxa in the genus. The number of significant discrepancies, relating to leaf morphology, floral morphology, and anatomy, between the two taxa are too many to conveniently fit the criteria of classification of infraspecific taxa that Stuessy (1990) recommends. Furthermore, they are not only sympatric in geographical and ecological distribution, but often grow physically adjacent to one another with minimal evidence of hybridisation. All practical aspects of the species concept proposed by Rollins (1951) and expanded by Futuyma & Mayer (1980) appear to have been satisfied.

The type of the species belongs in *H. pulvinaris* var. *pulvinaris*, so it is *H. pulvinaris* var. *minor* that must be promoted and renamed. Until such a time as the new species may be formally published (Todd & Ward, in prep.), it shall be referred to as *Haastia* species 'minor'.

Looking at the evidence gathered in this investigation, it appears that the type variety of *H. recurva* and *H. recurva* var. *wallii*, are not as distinct as is indicated by Cockayne (1918) and Allan (1961). A high degree of similarity between the Mt. Schiza population of var. *wallii* and at least one population of the type variety is indicated by the dendrogram, and the data certainly indicates that the leaf size of var. *wallii* is not significantly smaller than that of the type variety. However, given that the colour of the leaf is different, along with the shape of the bract apex, there appears to be no reason for the taxon not to retain its status. It must also be kept in mind that only one population of *H. recurva* var. *wallii* was sampled, and that greater discrepancies in leaf size may be apparent at sites that were not able to be visited.

The colour polymorphism evident in several North Canterbury populations of *H. recurva* seems to be simply that. There do not appear to be any other significant related discrepancies between the plants of each colour.

This investigation has confirmed that *Haastia sinclairii* exhibits a high degree of variability in several characters. While some variation of features between populations appear to be geographically consistent, such as the degree of blistering of the lamina surface, others, such as growth form do not. However, as noted above,

two populations, those of Mt. Terako and Mt. Barefell, emerge as being similar to one another and distinct from the rest of the species. Both the vegetative and floral parts are significantly larger than is common in other populations, the habit is consistently rhizomous, with the leaves held comparatively erect, and the involucral bracts are apiculate and binervate. The distribution may at least be described as peripatric with that of the main range of the species. These features indicate that the plants of these populations, and possibly others in the same area, may be classified as part of a new variety. This shall be referred to as *H. sinclairii* var. 'T' until formal publication (Todd & Ward, in prep.).

There is reason to speculate that the small cluster of populations of *H. sinclairii* in the vicinity of the Waimakiriri and Rakaia rivers (i.e. Craigieburn, Broken River and Mt. Hutt) could also be classified as a distinct variety, as they share a number of features in common that are not necessarily seen elsewhere. However, habit is not consistent between these populations, and there is the possibility that hybridisation with *H. recurva* is contributing to the unusual morphology. There is not enough conclusive evidence for formal recognition of this group at this stage.

Although the previously unrecognised taxon seen at Mt. Potts has been placed in *Haastia sinclairii* for the interim, it plainly does not belong there. Despite the fact that the habit and leaf size are similar to that of some forms of *H. sinclairii*, there are many qualitative discrepancies elsewhere. Such features as the elongation of the internodes of the floral shoots, the branching pattern of the veins of the involucral bracts, and the presence of canals in the leaf anatomy, none of which are seen elsewhere in *H. sinclairii*, all indicate that this taxon is something distinct.

Of added significance is the fact that a population of 'true' *H. sinclairii* grows close by, but does not intrude into the bowl in which the population was discovered. There is no evidence of hybridisation between the two.

The new taxon is itself unlikely to be a hybrid, although the latter two features mentioned above are shared with *H. recurva* and *H. pulvinaris* respectively. However, the nearest known population of *H. recurva* is over forty kilometres distant, at Mt. Hutt. The closest population of either of the pulvinate species is four times that distance away. Neither of these taxa are likely to have contributed to the creation of a hybrid population from those distances. Also, the population is quite well established, with over forty plants counted, and consistent of form throughout, a feature that was not encountered when interspecific hybrids of the genus were seen elsewhere. Finally, the elongation of the internodes of the floral shoots is unique in the genus. All other taxa have capitula that are sessile, or at least borne on shoots that appear no different to any others. It seems unlikely that such a character could have arisen as the result of hybridisation.

Such distinctive qualitative features, coupled with the known distribution of the plant, which is clearly sympatric with that of *H. sinclairii*, indicate that this form cannot be treated as an infraspecific taxon, but as a species in its own right. Even though the known range is presently extremely restricted, more populations may be located in suitable habitats in the surrounding region, particularly in the mountains of the Main Divide, to the north and west, and in the Taylor Range to the east.

Therefore, until a formal description is made (Todd & Ward, in prep.), this taxon shall be named *Haastia* species 'Potts'.

Finally, *H. sinclairii* var. *fulvida* exhibits such a number of features that distinguish it from the type form of *H. sinclairii* that promotion of the variety to the status of species may be considered. The lamina is longer and narrower than is seen elsewhere in the species, and also less hairy, the bract shape differs, and there are comparatively fewer palisade cells in the leaf. However, in comparison to the discrepancies between species elsewhere in the genus (particularly *H. sinclairii* and *H.* species 'Potts'), the distinction does not appear so large. Other than the character of bract shape, all the features listed above are quantitative, and may be explained by environmental adaptation and natural variation. Also, the geographical distribution of the variety appears to be allopatric, well separated from the range of the type variety in the north. This makes the degree of reproductive isolation of the taxon from the rest of the species difficult to evaluate without the benefit of glasshouse testing, as proposed by Rollins (1952). Until such a time as this may be investigated, the criteria of species suggested by Rollins (1952) and Futuyma & Mayer (1980) remain unsatisfied, and no promotion of *H. sinclairii* var. *fulvida* to the rank of species should be made.

Nor is promotion of *H. sinclairii* var. *fulvida* to the rank of sub-species necessarily advisable. Use of two categories below the rank of species, in the same species, would be unnecessarily complicated. Even though the variety shows comparatively greater divergence of form from that of the type than do other infraspecific taxa of the species, there is no compelling reason to promote it from its present rank.

Having elucidated the taxa of *Haastia* and their diagnostic features, it is now possible to study herbarium specimens of the genus and confidently name samples previously identified tentatively or incorrectly. Floral characters, such as the shape of the involucral bracts, are particularly useful in this respect. This will facilitate further study of the genus, its distribution, and its taxonomy.

5.6 Treatment of the genus

The results of the dendrogram indicate that the genus is divided in two, with the pulvinate species forming one part and the remainder of the species forming the other. Taken at face value, this supports the suggested treatment of Merxmüller *et al.* (1977), implying that the division may continue to the level of genus, and possibly even tribe. However, closer examination of a number of the morphological and anatomical features, such as the structure of the lamina surface, the arrangement and structure of the floral parts, and the presence of canals associated with the veins of the leaf, reveal links between the species that refute any major division of the genus.

The flavenoid analysis of the group, and the patterns of hybridisation seen, corroborate the view that the genus forms a monophyletic entity. There is no major departure from the basic pattern seen in the chromatograms that would suggest the presence of an unrelated group of compounds, although not all compounds are shared throughout the genus.

Interspecific hybridisation, while not overwhelmingly prevalent, is common enough to suggest that all of the various species are reasonably closely related, even between pulvinate and non-pulvinate species. In fact, as was pointed out previously, it was specimens of precisely this hybrid combination that were most conspicuous in the field.

In short, there is no reason to believe that the two parts of the genus are the result of morphological convergence, or that there is any necessity for the creation of a new genus.

The evidence of this investigation appears to only partially satisfy the treatment of Bremer (1994), in that only one of the two style types, sapexulated (continuous stigmatic surface, coupled with dorsal hairs), was noted throughout the entire genus. This does not follow Bremer's treatment, which suggests that both style types should be present.

5.7 Further Research

Due to restrictions of publication, this is not a formal revision of the genus *Haastia*. However, such a revision is planned for the future, in which the new taxa will be named and formally described.

Further research into the relationship of *Haastia* with other endemic composite genera, and possibly genera from elsewhere in the world, is evidently necessary. This research should not only be morphological and anatomical in nature; molecular and biochemical analysis may also provide useful insights.

Other research that may prove useful in this respect is an investigation of the biogeographical and evolutionary history of the genus, through examination of the fossil record. This may provide some clues as to the possible origins of *Haastia*. In relation to this, a study of the pollination biology and current evolutionary processes of the genus would be useful, particularly if this were carried out in conjunction with on going research into the endemic genera of the Inuleae and other composites.

References

Allan, H. H. (1961): *Flora of New Zealand.* Vol. I. Government Printer, Wellington.

Anderberg, A. A. (1989): Phylogeny and reclassification of the tribe Inuleae (Asteraceae). *Can. J. Bot.* 67: 2277-2296.

--- (1991): Taxonomy and phylogeny of the tribe Gnaphaliinae (Asteraceae). *Opera Botanica* 104: 1-195.

Arnold, M.L. (1994): Natural hybridisation and Louisiana Irises. *Bioscience* 44: 141-147.

Bentham, G. (1873): Mr. G. Bentham on Compositae. *Bot. J. Linn. Soc.* 13: 335-577.

Boyd, A.; Wood, C.(1969): Preparation of animal tissue for surface-scanning electron microscopy. *J. Microsc.* 90: 221

Breitwieser, I. (1993): Comparative leaf anatomy of New Zealand and Tasmanian Inuleae (Compositae). *Bot. J. Linn. Soc.* 111: 183-209.

Breitwieser, I.; Ward J.M. (1993): Systematics of the New Zealand Inuleae (Compositae-Asteraceae)-3. Numerical phenetic analysis of leaf anatomy and flavonoids. *N. Z. J. Bot.* 31: 45-58

Bremer, K. (1994): *Asteraceae Cladistics and Classification.* Timber Press, London.

Buchanan, J. (1882): On the alpine flora of New Zealand. *Trans. N. Z. Inst.* 14: 342-356

--- (1887): On some new native plants. *Trans. N. Z. Inst.* 19: 213-216

Burger, W. C. (1975): The species concept in *Quercus*. *Taxon* 24: 45-50.

Burrows, C.J. (1967): Progress in the study of South Island alpine vegetation. *Proc. N. Z. Ecol. Soc.* 14: 8-13.

Cheeseman, T.F. (1925): *Manual of the New Zealand Flora.* 2nd edition. Government Printer, Wellington

Cockayne, L. (1918): Notes on New Zealand floristic botany, including descriptions of new species (No. 3). *Trans. N. Z. Inst.* 50: 160-191.

Cockayne, L; Allan, H.H. (1934): An annotated list of groups of wild hybrids in the New Zealand flora. *Ann. Bot., Lond.* 48: 1-55

Davis, P.H.; Heywood, V.H. (Eds.) (1963): *Principles of Angiosperm Taxonomy.* Oliver and Boyd, Edinburgh and London.

Drury, D.G. (1970): A fresh approach to the classification of the genus *Gnaphalium*, with particular reference to the species present in New Zealand (Inuleae-Compositae). *N. Z. J. Bot.* 8: 222-248.

Duncan, T.; Baum, B.R. (1981): Numerical phenetics: its uses in botanical systematics. *Ann. Rev. Ecol. Syst.* 12: 387-404.

Duncan, T.; Stuessy, T.F. (1985): *Cladistic Theory and Methodology.* Van Nostrand Reinhold, New York.

Du Rietz, G.E. (1930): The fundamental units of biological taxonomy. *Svensk Bot. Tidskr.* 24: 333-428.

Ehrlich, P.R. (1961): Has the biological species concept outlived its usefulness? *Syst. Zoo.* 10: 167-176.

Eldredge, N.; Gould, S.J. (1972): Punctuated equilibria: an alternative phyletic gradualism. In: *Models in Paleobiology* (Ed.: Schopf, T.J.M.). Freeman, San Francisco: 82-115.

Funk, V.A.; Brooks, D.R. (1981): Foreword. In: *Advances in Cladistics.* New York Botanical Garden, New York: v-vi.

Futuyma, D.G.; Mayer G.C. (1980): Non-allopatric speciation in animals. *Syst. Zoo.* 29: 254-271.

Gardner, E.J.; Snustad, D.P. (1984): *Principles of Genetics.* 7th edition. Wiley, New York.

Gower, J.C. (1971): A general coefficient of similarity and some of its properties. *Biometrics* 27: 857-874.

Grant, V. (1971): *Plant Speciation.* Columbia University Press, New York.

Harborne, J.B.; Turner, B.L. (1984): *Plant Chemosytematics.* Academic Press, London.

Heiser, C.B. (1973): Introgression re-examined. *Bot. Rev.* 39: 347-366.

Hennig, W. (1965): Phylogenetic systematics. *Ann. Rev. Entomol.* 10: 97-116.

--- (1966): *Phylogenetic Systematics.* Trans. by Davis, D.D.; Zangerl, R. University of Illinois Press, Urbana.

Heywood, V.H. (1967): Variation in species concepts. *Bull. Jard. Bot. Etat* 37: 31-36.

Hilliard, O.M.; Burtt, B.L. (1981): Some generic concepts in Compositae-Gnaphaliinae. *Bot. J. Linn. Soc.* 82: 181-232.

Hooker, J.D. (1864): *Handbook of the New Zealand Flora.* Reeve, London.

--- *in* Kirk, T. (1899): *The Students Flora of New Zealand.* Government Printer, Wellington.

Huxley, J. (1942): *Evolution: the modern synthesis.* Allen & Unwin, London.

Kay, Q.O.N. (1976): Preferential pollination of yellow-flowered morphs of *Raphanus raphanistrum* by *Pieris* and *Eristalis* spp. *Nature* 261: 230-232.

Kavanaugh, D.H. (1977): Hennigian phylogenetics in contemporary systematics: principles, methods, and uses. In: *Biosystematics in Agriculture* (Ed.: Romberger, J.A.) Allanheld, Osmun & Co., New York: 139-150.

Kennington, A.L. (1978): *The Awatere: a district and its people.* Marlborough County Council, Blenheim.

Kirk, T. (1899): *The Students Flora of New Zealand.* Government Printer, Wellington.

Laing, R.M. (1912): Some notes on the botany of the Spenser Mountains with a list of species collected. *Trans. N. Z. Inst.* 44: 60-75.

de Laubenfels, D.J. (1969): A revision of the Malesian and Pacific rainforest conifers, 1. Podocarpaceae, in part. *J. Arnold Arb.* 50: 274-369.

Littlejohn, M.J. (1981): Reproductive isolation: a critical review. In: *Evolution and Speciation: Essays in Honour of M.J.D. White.* (Eds.: Atchley, W.R.; Woodruff, D.S.). Cambridge University Press, Cambridge: 298-334.

Low, E. (1899): On the vegetative organs of *Haastia pulvinaris. Trans. N. Z. Inst.* 31, 150-157.

Mabry, T.J.; Markham, K.R.; Thomas, M.B. (1970): *The systematic identification of flavonoids.* Springer Verlag, Berlin.

Mark, A.F.; Adams, N.M. (1973): *New Zealand Alpine Plants.* Godwit, Auckland.

Markham, K.R. (1982): *Techniques of flavonoid identification.* Academic Press, London.

Markham, K.R.; Webby, R.F.; Whitehouse, L.A.; Molloy, B.P.J.; Vilain, C.; Mues, R. (1985): Support from flavonoid glycoside distribution for the division of *Podocarpus* in New Zealand. *N. Z. J. Bot.* 23: 1-13.

Mayr, E. (1940): Speciation phenomena in birds. *Am. Nat.* 74: 249-278.

--- (1942): *Systematics and the Origin of Species.* Columbia University Press, New York.

--- (1963): *Animal Species and Evolution.* Belknap Press, Cambridge, Mass.

Merxmüller, H.; Leins, P.; Roessler, H. (1977): Inulae-systematic review. In: *The Biology and Chemistry of the Compositae* (Eds.: Heywood, V.H.; Harborne, J.B.; Turner, B.L.). Academic Press, London: 577-602.

Rathcke, B.; Lacey, E.P. (1985): Phenological patterns of terrestrial plants. *Ann. Rev. Ecol. Syst.* 16: 179-214.

Reiseberg, L.H.; Ellstrand, N.C. (1993): What can molecular and morphological markers tell us about plant hybridisation? *Critical Reviews in Plant Sciences* 12: 213-241.

Rollins, R.C. (1952): Taxonomy today and tomorrow. *Rhodora* 52: 1-19.

Runemark, H. (1961): The species and sub-species concept in sexual flowering plants. *Bot. Not.* 114: 22-42.

Simpson, G.G. (1961): *Principles of Animal Taxonomy.* Columbia University Press, New York.

Sneath, P.H.A.; Sokal, R.R. (1973): *Numerical Taxonomy.* W.H. Freeman & Co., San Francisco.

Sokal, R.R.; Sneath, P.H.A. (1963): *Principles of Numerical Taxonomy.* W.H. Freeman & Co., San Francisco.

Stebbins, G.L. (1950): *Variation and Evolution in Plants.* Columbia University Press, New York.

Stevens, P.F. (1980): Evolutionary polarity of character states. *Ann. Rev. Ecol. Syst.* 11: 333-358.

Stuessy, T. F. (1990): *Plant Taxonomy: The Systematic Evaluation of Comparative Data.* Columbia University Press, New York.

Turner, R.H.; Green, C.D. (1973): Preparation of biological material for scanning electron microscopy by critical point drying from water miscible solvents. *J. Microsc.* 97: 357-363.

Webb, C.J. *in* Webb, C.J.; Sykes, W.R.; Garnock-Jones, P.J. (1988): *Flora of New Zealand.* Vol. IV. Botany Division, DSIR, Christchurch.

Appendix I

Key to Taxa

1. (a) Growth form pulvinate 2.

   (b) Growth form non-pulvinate 3.

2. (a) Branchlets <15mm diam.; leaves yellow-green, flabellate, apex rounded; involucral bracts obovate *H. pulvinaris*

   (b) Branchlets up to 20mm diam.; leaves gold or buff, subflabellate, apex truncate; involucral bracts ovate *H.* species 'minor'

3. (a) Growth form decumbent; leaves < 15mm long; leaf internodes < 1mm; pappus united 4.

   (b) Growth form decumbent, sprawling or rhizomatous; leaves reaching lengths > 20mm; leaf internodes reaching lengths > 2mm; pappus free 5.

4. (a) Leaves silver or bronze, recurved up to 75°; capitula up to 10mm diam.; involucral bract tips acute *H. recurva* var. *recurva*

   (b) Leaves yellow-green, recurved up to 90°; capitula < 6mm diam.; involucral bracts apiculate *H. recurva* var. *wallii*

5. (a) Growth form decumbent, sprawling, or rhizomatous; capitula sessile; involucral bracts linear 6.

(b) Growth form decumbent; floral stems elongated; involucral bracts elliptic

H. species 'Potts'

6. (a) Growth form decumbent, sprawling or rhizomatous; leaves silver or grey; leaf hairs dense 7.

(b) Growth form decumbent or sprawling; leaves green; leaf hairs sparse

H. sinclairii var. *fulvida*

7. (a) Growth form decumbent, sprawling or rhizomatous; leaves < 20mm long, apex acute to rounded, silver or grey; capitula < 15mm diam.; involucral bracts up to 15mm long, apex acute *H. sinclairii* var. *sinclairii*

(b) Growth form rhizomatous; leaves up to 30mm long, apex rounded, silver; capitula up to 30mm diam.; involucral bracts up to 20mm long, apex apiculate

H. sinclairii var. 'T'

Descriptions of taxa

Haastia: Leaves sheathing, persistent; lamina thickened, lanate, dorsal surface rugose to crenellate; sheath lanate without; major veins 3-10, secondary veins numerous, reticulate. Capitula solitary, terminal, heterogamous; involucral bracts in 2 series, senescent at tips and upper margins, lanate without; receptacle small, flat or convex; florets tubular; outer florets pistillate, numerous, corolla reduced; inner florets perfect, numerous; anthers ± obtuse at base; styles bifurcate, style arms of hermaphrodite florets ± papillose at tips, style arms of female florets glabrous; stigmatic surface continuous. Pappus of one series of long, rigid hairs.

Achenes oblong, compressed to cylindrical, glabrous. Sub-shrubs or herbs, somewhat woody in stem bases.

H. pulvinaris: Plant pulvinate, very densely branched, cushion surface uniform, up to 2m in diam. Branchlets up to 15mm in diam.; leaves tightly appressed, tips distinct; internodes negligible. Leaves yellow-green, subflabellate, 6-8mm long x 8-12mm wide; hairs *c.* 2mm long, dense; lamina thickened, ventral surface crenellate, strongly recurved, apex rounded; major veins 3-5, secondary veins numerous. Capitula 7-8mm in diam., sessile, receptacle 5-7mm in diam.; involucral bracts obovate, 5-8mm long with 1-2 simple veins, apex acute. Corolla of female florets reduced to *c.* three fifths length of style; style arm of hermaphrodite florets caespitose at apices; pappus hairs free at base, 6-7mm long.

H. *species 'minor'*: Plant pulvinate, very densely branched, cushion surface uniform to undulating, up to 1.5m in diam. Branchlets up to 20mm in diam; leaves tightly appressed, tips indistinct; internodes negligible. Leaves buff to gold, subflabellate, 6-9mm long x 5-9mm wide; hairs 2-3mm long, very dense; lamina thickened, ventral surface strongly crenellate, strongly recurved, apex truncate; major veins 3, secondary veins numerous. Capitula 5-7mm in diam., sessile, receptacle 4-6mm in diam.; involucral bracts ovate, 6-7mm long with 1-2 simple veins, apex acute. Corolla of female florets reduced to *c.* three fifths length of style; style arm of hermaphrodite florets papillose at apices; pappus hairs free at base, 6-7mm long.

H. recurva *var.* recurva: Plant decumbent, sparsely to densely branched, stems up to *c.*30cm. long Leaf internodes *c.* 1mm long. Leaves silver or bronze, obovate, 13-18mm long x 6-9mm wide; hairs 1-2mm long, dense; lamina thickened, bullate, recurved, apex obtuse to rounded; major veins 3, secondary veins numerous. Capitula 8-10mm in diam., sessile; receptacle 7-9mm in diam.; involucral bracts linear, 9-11mm long with single branching vein, apex acute. Corolla of female florets reduced to base of style; style arms of hermaphrodite florets papillose at apices; pappus hairs connate at base, 9-10mm long.

H. recurva *var.* wallii: Plant decumbent, densely branched, stems up to *c.* 20cm long. Leaf internodes *c.* 1mm long. Leaves yellow-green, obovate, 14-15mm long x 6-7mm wide; hairs 1-2mm long, dense; lamina thickened, bullate, strongly recurved, apex obtuse; major veins 3, secondary veins numerous. Capitula 6-7mm in diam., sessile; receptacle 5-6mm in diam.; involucral bracts linear, 9-10mm long with single simple vein, apex apiculate. Corolla of female florets reduced to base of style; style arms of hermaphrodite florets papillose at apices; pappus hairs connate at base, 8-9mm long.

H. sinclairii *var.* sinclairii: Plant sprawling to decumbent or rhizomatous, sparsely to densely branched or clumped 2-3, stems 10-30cm long. Leaf internodes up to 5mm long. Leaves silver to grey, obovate, 18-25mm long x 9-12mm wide; hairs 2-3mm long, dense; lamina ± thickened, rugose to bullate, ± patent, apex obtuse to rounded; major veins *c.*5-7, secondary veins sparse to numerous. Capitula 9-12mm in diam., sessile; receptacle 6-9mm in diam; involucral bracts linear, 10-12 mm long with single simple vein, apex acute. Corolla of female florets reduced

to base of style; style arms of hermaphrodite florets subpapillose at apices; pappus hairs free at base, 9-10 mm long.

H. sinclairii *var.* fulvida: Plant sprawling to decumbent, sparsely to densely branched, stems *c.* 30cm long. Leaf internodes 3-5mm long. Leaves yellow-green to green, obovate, 25-35mm long x 10-12mm wide; hairs *c.* 2mm long, sparse; lamina not thickened, rugose, slightly recurved, apex rounded; major veins *c.* 5-7, secondary veins numerous. Capitula 9-12mm in diam., sessile; receptacle 8-10mm in diam; involucral bracts linear, thickened in lower section, 8-10mm long with 1-2 simple veins, apex acute. Corolla of female florets reduced to *c.* two fifths length of style; style arms of hermaphrodite florets subpapillose at apices; pappus hairs free at base, 7-9mm long.

H. sinclairii *var.* *'T'*: Plant rhizomatous, stems solitary or clumped 2-3, up to 3cm tall. Leaf internodes 1-2mm long. Leaves silver, obovate, 20-25mm long x 12-14mm wide; hairs 1-2mm long, dense; lamina thickened, rugose, erect, apex obtuse to rounded; major veins *c.* 5-7, secondary veins numerous. Capitula up to 30mm in diam., not elevated above foliage; receptacle 11-15mm in diam., involucral bracts linear, 15-20mm long with single simple vein, apex apiculate. Corolla of female florets reduced to *c.* half length of style; style arms of hermaphrodite florets caespitose at tips; pappus hairs free at base, 15-18mm long.

H. *species 'Potts'*: Plant decumbent, densely branched, vegetative stems up to 20cm long, floral stems 20-25cm long. Leaf internodes 1-2mm long, 3-4mm long on floral stems. Leaves yellow-green, obovate, 18-20mm long x 8-10mm wide,

hairs 1-2mm long, dense; lamina ± thickened, rugose, patent, apex rounded; major veins *c.* 5-9, secondary veins numerous. Capitula 10-12mm in diam., elevated; receptacle 8-10mm in diam.; involucral bracts elliptic, 9-10mm long with single branching vein, apex acute. Corolla of female florets reduced to *c.* two fifths length of style; style arms of hermaphrodite florets papillose at tips; pappus hairs free at base, *c.* 10mm long.

Appendix II

Collecting Sites

Site	Location	Map Reference
Kakapo Peak	Douglas Range, NW Nelson	NZMS260-M32: 548-368
Tapu-ea-nuku	Inland Kaikoura Range, Marlborough	NZMS260-O30: 632-139
Mt. Schiza	Raglan Range, Marlborough	NZMS260-O29: 305-284
Mt. Barefell	Rachel Range, Marlborough	NZMS260-N30: 224-942
Mt. Fyffe	Seaward Kaikoura Range, Marlborough	NZMS260-O31: 615-789
Balaklava Ridge	Crimea Range, Nelson	NZMS260-N30: 977-932
Mt. Southey	Turk Ridge, Nelson	NZMS260-M30: 895-902
Mt. Princess	St. James Range, Nelson	NZMS260-M30: 841-912
Mt. McCabe	St. James Range, Nelson	NZMS260-M30: 859-903
Mt. Terako	Amuri Range, North Canterbury	NZMS260-N31: 216-625
Mt. St. Patrick	Hanmer Range, North Canterbury	NZMS260-M31: 876-623
Mt. Edison	Glynn Wye Range, North Canterbury	NZMS260-M32: 547-369
Poulter Range	Poulter Range, North Canterbury	NZMS260-L33: 226-237
Poulter Hill	The Candlesticks, North Canterbury	NZMS260-L33: 280-116
Craigieburn	Craigieburn Range, Canterbury	NZMS260-K34: 033-869
Broken River	Craigieburn Range, Canterbury	NZMS260-K34: 042-881
Mt. Hutt	Mt. Hutt Range, Mid Canterbury	NZMS260-K35: 912-449
Mt. Potts	Potts Range, Mid Canterbury	NZMS260-J35: 912-449
Ohau	Barrier Range, South Canterbury	NZMS260-H38: 520-592
Mt. Bonpland	Humboldt Range, Fiordland	NZMS260-E40: 352-925

Appendix III

The computer disc attached contains two data files and one program, named 'pop.csv' and 'phen.csv', and 'gower' respectively. The data files contain the actual data used in the numerical phenetic analysis, and the data recorded during the observations of flowering times on Mt. St. Patrick. The data in 'pop.csv' differs little from that in the tables presented in Chap. 4, save that it is in a format compatible with the program 'gower'. In addition, any data relating to ratios between measurements is log transformed, in order to present a linear relationship between data points.

'Gower' is the program written to calculate the similarity values for each OTU, using this data.

Both 'pop.csv' and 'phen.csv' may be viewed using Microsoft Excel. 'Gower' is written in FORTRAN, and is used in MS DOS.

Acknowledgements

The completion of this thesis would not have been possible without the co-operation and assistance of a number of parties, to whom I now express my gratitude.

To my supervisor, Dr. Josephine Ward, I direct warmest thanks and appreciation for her guidance and patience over the last two years. Without her knowledge and experience, this project would have foundered very quickly.

My thanks to the members of the Botanical Societies of Wellington and Canterbury for their willingness to provide financial assistance. The funds gifted by these organisations eased the expense of field work considerably.

I should like to thank the owners and management of the following properties for their co-operation in allowing me access to their land in order to carry out the necessary field work; Gladstone Downs Station, Glazebrook Station, Stronvar Station, Mt. Lyford Station and Ski-field, St. James Station, Amuri Ski-field, Glynn Wye Station, Mt. White Station, Craigieburn Valley Ski-field, Broken River Ski-field, Mt. Hutt Ski-field, Mt. Potts Station, Erewhon Park Ski-field, and Routeburn Station.

Similarly, I should like to thank the staff of the Canterbury and Nelson/Marlborough Conservancies of the Department of Conservation, for allowing me to make collections from sites on land in those regions administered by D.o.C. My particular

thanks must go to Shannel Courtney, the Botanical Officer for Nelson/Marlborough, for his personal assistance and willingness to share his knowledge of the genus.

The staff of Landcare Research, at Lincoln, offered me assistance in my investigation of the herbarium material, for which I am most grateful. I must especially thank Dr. Ilse Breitwieser, Dr. Steve Wagstaffe, and Briony Macmillan for their advice and insights.

I must tender my thanks to the staff of the Departments of Plant and Microbial Sciences, and of Zoology, at the University of Canterbury, for the technical assistance and advice that I have received over the course of the investigation. My special thanks go to Reijel Gardener, for her help in the preparation of tissue sections, Karen Baas, for her help in the preparation of chromatograms, Dougal Holmes, for his help with photography, and Maggie Tisch, for whom no request was too great a problem!

I could not have achieved the amount of field-work that I did without the willing help of a number of field assistants who gave up their time to join me on various trips; Simon Atkins, Monique Baars, Remco Baars, Dr. Colin Burrows, Angela Cone, Michael Croxton, Timothy Jordan, Susan Marks, William Murray, Philip Tisch, and Dr. Ashley Sparrow. I cannot thank these people enough, their help was invaluable.

I should also like to thank Ashley Sparrow for his willingness to moonlight as a statistical consultant and computer programmer. I'm sure that I'll understand the theory of the techniques and tests that he showed me some day!

Several people offered me criticism and advice while the document was in the process of being written, most of which was taken on board. I should like to thank Professor John Lovis, Trevor Lyttle, Marcus Reut, and Andrea Thom for their perspectives and their expertise, both of which were greatly valued.

My greatest appreciation must go to Aaron Wilton, who constantly and consistently provided assistance, advice, criticism and insights at all stages of this study. He was invaluable in the field and the laboratory, made useful comments on my ideas and techniques, and was generally helpful at all times. I hope that I can return the service at some time in the future.

Finally, I must give thanks to my parents, who made me seriously consider my options before committing myself to this project, but then gave me their full support once I had made my decision. Thank you both.